

Planning Context and Foundation

Chapter 1:
Introduction

Chapter 2:
Patterns of Habitat Use by Lynx and
Snowshoe Hare

SECTION ONE

Chapter 1:

INTRODUCTION

This chapter introduces the species of concern, highlights the planning context, and identifies the planning considerations that influenced this document. In the first section, lynx are briefly described, their distribution is discussed, and highlights of lynx natural history are noted. The second and third sections identify the context in which this plan was developed, including both the conservation issues that initiated concern for the species and the eventual role of DNR in special lynx habitat management. In the final section, general assumptions are listed that identify the philosophies behind the plan. Stemming from these assumptions, the multi-scaled organizational structure used throughout the plan is also introduced.

1.1 The Species

1.2 Current Status and Conservation Issues

1.3 DNR's Role in Lynx Habitat Management

1.4 Planning Considerations

1.1 The Species: *Lynx Canadensis*¹

1.1.1 Description

Smaller than cougars but slightly larger than bobcats, the 15-30 pound (6.8-13.6 kg) lynx are characterized by a short and black-tipped tail, tufted ears, facial ruff, elongated hind legs, and large paws. Lynx are relatively common predators throughout Alaska and most of Canada (Fed. Register 1994, Koehler and Aubry 1994), where their snowshoe-like paws enable them to traverse boreal forests in search of their favored prey, the snowshoe hare. These specialized paws enable lynx to exploit habitat often avoided by other predators, whose movements are more inhibited by deep snow. For example, bobcats, cougars, and coyotes at the southern edge of lynx range winter on south-southwest aspects, approximately 300-400 feet (984-1312 m) lower than lynx (Koehler and Hornocker 1991, Koehler 1990a).² Many attributes of the lynx's natural history are closely tied to the distribution, persistence, and abundance of the snowshoe hare. Refer to Tumilson (1987), Hatler (1988), Washington Department of Wildlife [WDW] (1993), Butts (1992), and Koehler and Aubry (1994) for natural history descriptions, and to Weaver (1993) for a research assessment.

1.1.2 Distribution

The range of the lynx encompasses the Canadian and Hudsonian life zones (Ingles 1965) of boreal North America (Fig. 1). Over 80% of this area lies within Canada. Of the portion remaining, over 2/3 occurs in Alaska, leaving approximately 6% of the total species range in the conterminous United States. Lynx range in Washington represents approximately 0.5% of the total area occupied by lynx. However, Washington may support a significant proportion of the resident populations of lynx in the conterminous United States. Both Washington (Brittell et al. 1989) and Montana (Giddings 1994) claim to have the largest breeding populations of lynx south of Canada.

Within Washington, lynx occupy high elevation coniferous forests where heavy snows accumulate (WDW 1993). There are six recognized zones of primary lynx habitat (WDW 1993, Fig. 2). Also, recent records from central Washington Cascades (i.e. Yakima Co., Nov. 1991;

¹Scientific names are presented in Appendix A; mammalian taxonomy follows Wilson and Reeder (1993).

²Competition among these predators may also influence habitat use. Nonetheless, the greater surface area of a lynx paw can support twice the weight of a bobcat paw (Parker et al. 1983) and 3.4-8.1 times the foot load of a coyote paw (Murray and Boutin 1991).

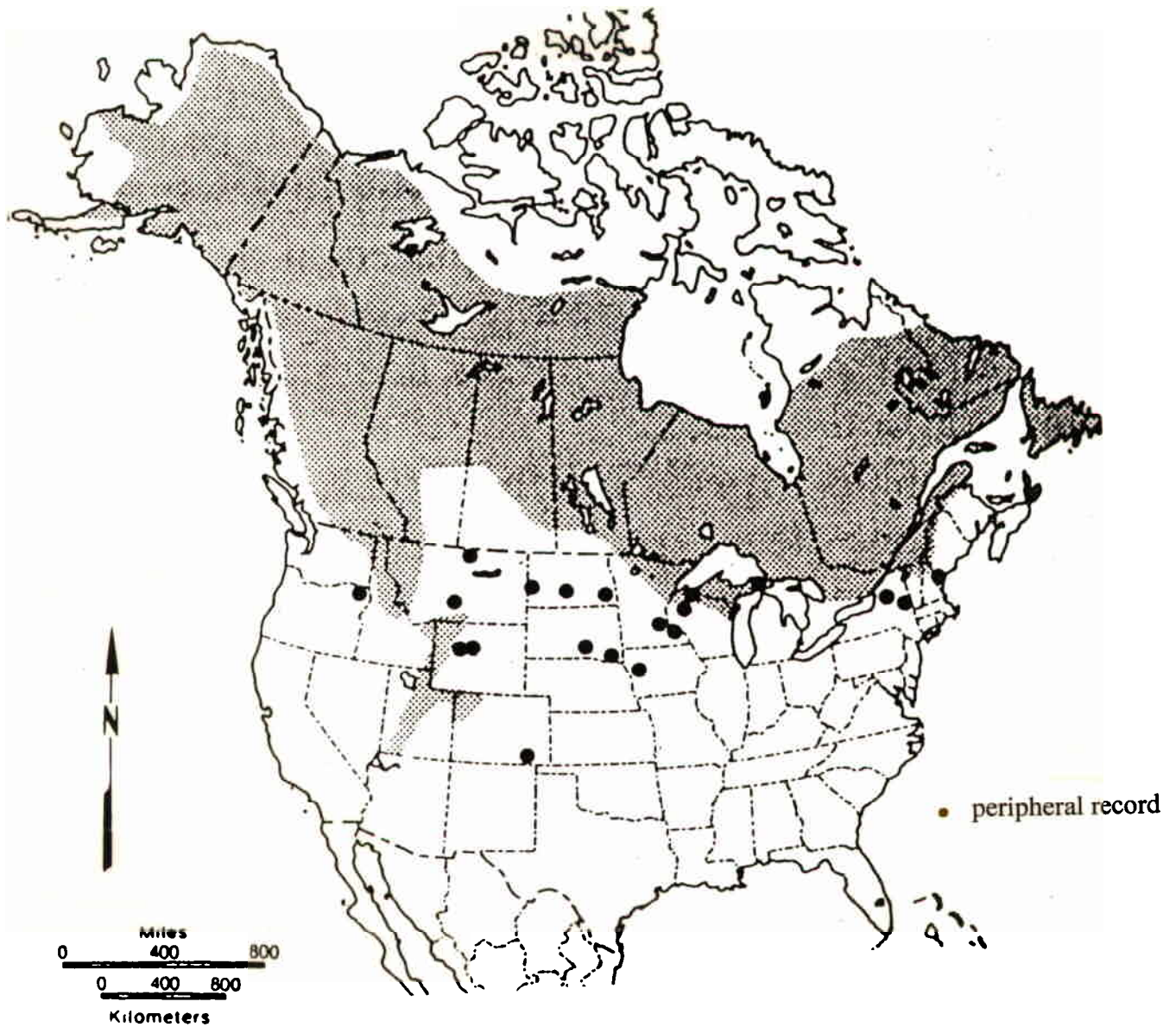


Figure 1: Distribution of the lynx, *Lynx canadensis* (adapted from McCord and Cardoza 1982).

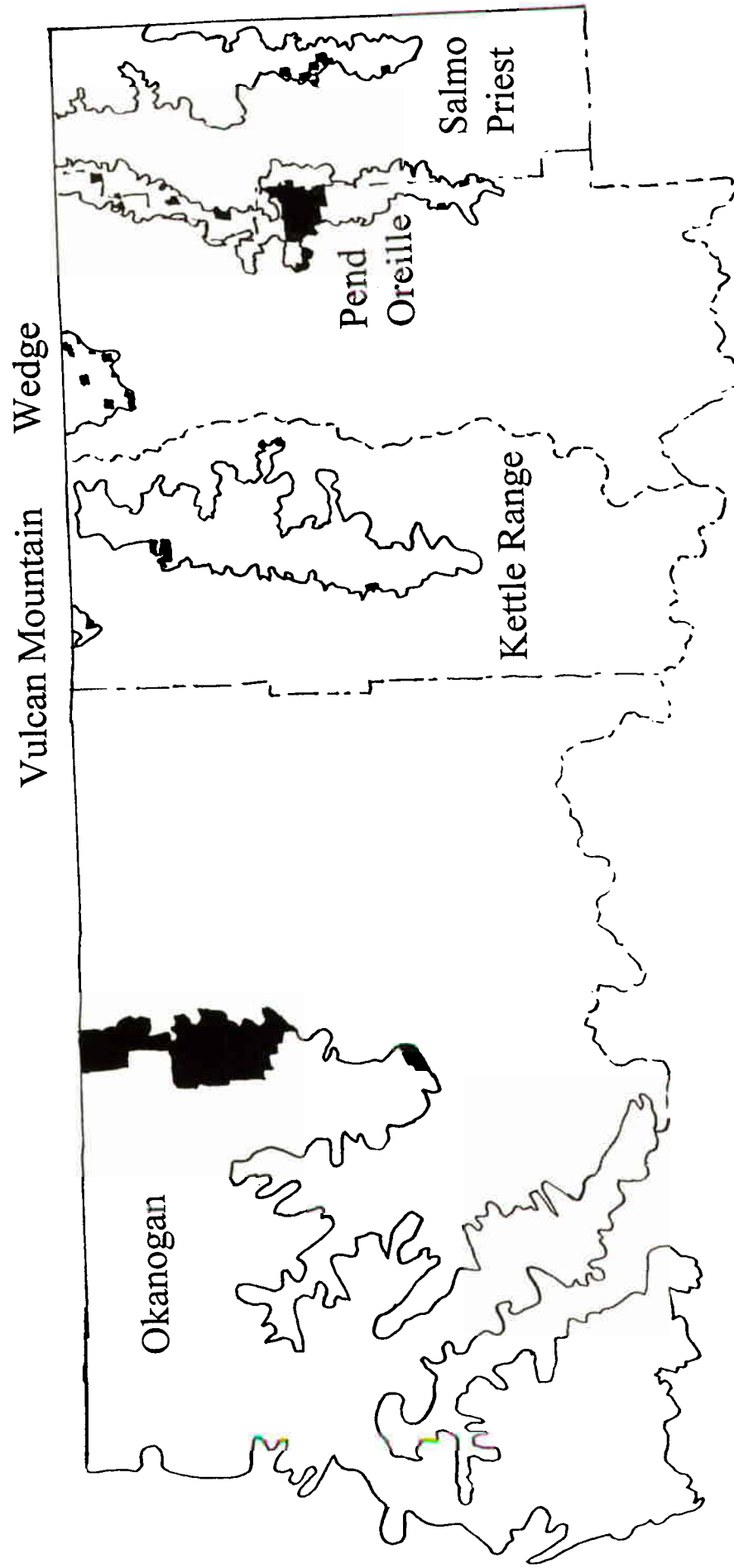


Figure 2: Primary distribution of lynx in Washington, the six Lynx Management Zones (WDW 1993).

WDW 1993) and historical records from the Blue Mountains of southeastern Washington indicate the presence of lynx outside of these areas.

1.1.3 The Prey

Lynx are perhaps best known for their unique association with a single prey item, the snowshoe hare. Ecologists have focused on this predator-prey system since it was popularized in the 1940's (e.g. Elton and Nicholson 1942), developing a large quantity of literature and inspiring many theoretical hypotheses (review, Keith 1963; Keith et al. 1984; Krebs et al. 1991, 1995; Sinclair et al. 1993). The lynx literature is nearly unanimous in concluding that hares are the main prey of lynx in all seasons (by rank), although snow-free season samples are relatively rare. Not only are hares found in scats with frequencies of 35% (during a low in hare abundance, Brand and Keith 1979) to 100% (Kesterson 1988) and volumes in stomach and intestine samples of 41% (Saunders 1963a) to 100% (Brand et al. 1976), but the loss of body fat by lynx during periods of low hare density indicates that they might not be able to consume enough alternative prey (e.g. grouse, squirrels, and carrion) to meet their energy requirements (Brand and Keith 1979).

There is clear evidence of opportunism in lynx prey selection, especially when hares are at low densities and during the summer. For example, high frequencies of red squirrels in lynx diets have been reported from Washington (Koehler 1990a), Yukon (M. O'Donoghue, Univ. British Columbia, pers. commun.), and Alaska (Staples 1995). Lynx consumption of caribou, Dall sheep, and red foxes was reviewed by Stephenson et al. (1991). One of the most famous examples of lynx as predators on non-hare prey is from Newfoundland, where lynx had a dramatic and publicized effect on caribou herds (Bergerud 1971, 1983). Examples of seasonal opportunism include an increase in diet diversity with prey availability during summer (Saunders 1963a, van Zyll de Jong 1966, Brand et al. 1976, Parker et al. 1983, Staples 1995) and a reliance on moose carrion (70%) when it was readily available near a hunting camp in fall (Saunders 1963a). Despite this opportunism, lynx density oscillates with the density of snowshoe hare through changes in reproduction and survival patterns, especially through reproductive success of yearlings and survival of kittens (see Koehler and Aubry 1994, for review; Mowat 1993, O'Conner 1984).

The critical association between lynx and snowshoe hare is the high correlation between lynx recruitment and winter/early spring snowshoe hare abundance (e.g. Nellis et al. 1972, Brand and Keith 1979, Parker et al. 1983, O'Conner 1984, Mowat 1993, Poole 1994). Winter is likely the constraining season in hare populations (Walski and Mautz 1977, Krebs et al. 1986, Krebs et al. 1991) due to the high metabolic requirements of homeothermy during extreme cold temperatures

combined with a relative lack of browse.³ Periods of unusually cold weather have been correlated with increased mortality rates in both species (hare: Meslow and Keith 1971, Pease et al. 1979; lynx: Poole 1994). Aside from hare, ptarmigan, grouse, and red squirrels, the boreal forest offers few prey choices for lynx and other carnivores during winter (van Zyll de Jong 1966). Ground squirrels and marmots hibernate, birds migrate, and ungulate calves don't appear until spring. The availability of mice, voles, and pikas is reduced due to snow cover. Of the three food choices that remain accessible, hares are usually the most abundant. Thus, the persistence of lynx has become entwined through time with the persistence of hare.

1.2 Current Status and Conservation Issues

The lynx was listed as threatened in the state of Washington in October 1993, by the Washington State Wildlife Commission. Although the U.S. Fish & Wildlife Service [USFWS] determined that listing lynx as threatened or endangered was not warranted (Fed. Register 1994), letters exchanged by carnivore experts and region offices of the USFWS (J. Weaver; G. Koehler; M. Hornocker, Hornocker Wildl. Res. Institute; and USFWS, letters on file) indicate disagreement on the status of lynx within the coterminous United States. The role of the northern states as sinks for lynx emigrating from Canada during lynx population highs or when snowshoe hare abundance declines is recognized (e.g. Banfield 1974, Mech 1980; see Koehler and Aubry 1994 for review), but the role of these areas in independently supporting breeding populations of lynx is less understood (see Fed. Register 1994). Biogeographic theory warns that peripheral, low density populations are naturally subject to increased risk of local extinction (for a brief review, see Weaver 1993).

Whether Washington and other southern lynx habitats support persistent breeding populations, they retain importance to the species. As argued by J. Weaver and G. Koehler (letters on file), habitats occupied at periodic intervals are part of the species range, whether the interval is once a decade, like lynx, or once a year, like neotropical migrant birds. Also, the juxtaposition of plant and animal species associated with boreal and southern forests that occurs in the northern states affords a unique research setting. Ecological, social, and physiological adaptations and habitat

³Winter is not considered the constraining season for lynx recruitment because continued parturition (Mowat 1993), ovulation, and implantation (Brand and Keith 1979, Parker et al. 1983, O'Conner 1984) indicate that adult, resident lynx breed during years with low hare abundance. However, most of the kittens born under such conditions do not survive (Mowat 1993, Mowat et al. 1996). Survival of kittens is therefore higher during the snow than snow-free season (Mowat 1993, Mowat et al. 1996). However, the snow season indirectly constrains lynx through its effects on the snowshoe hare. Low food supply likely depresses the ability of breeding females to lactate and increases predation pressure on kittens during the start of the snow-free season.

preferences may become more apparent as the contrast between preferred-versus-available habitat increases in southern latitudes.

Habitat and conservation issues throughout the range of the lynx have become an increasing concern as decreases in sightings and fur harvests are reported and human populations expand into remote lynx country. Many locations reported lower fur harvests in the 1980's compared with the 1970's: Alberta (Todd 1985), Washington (Brittall et al. 1989 and Koehler 1990a), Montana (Hash 1990, Roy 1990), Alaska (Stephenson 1986), Manitoba (McKay 1985), British Columbia (Hatler 1988). All of the authors suspected that the declines were at least partially due to over trapping in the 1970's, when pelt prices were relatively high.⁴ The Lynx Management Guidelines of British Columbia (B.C. Ministry of Environment) describe a double peak in the seventies (1972-73 and 1973-74), where over 8,500 pelts were sold each year. On the Kenai National Wildlife Refuge, the lynx fur harvest of 1973-1974 was 40 times greater than 1966-1967 (Bailey 1981). In Washington, the number of individuals trapped was three-fold higher in the 1970's (146 animals, from the 1969-70 harvest to the 1977-78 harvest) than the 1960's (44 animals, 1960-61 harvest to the 1968-69 harvest). Sighting records similarly indicate a decline in lynx abundance over the past ten years, although lynx distribution has remained approximately the same (WDW 1993).

Although untrapped lynx populations may undergo dramatic losses from natural mortality during hare lows (19/27 known deaths in Northwest Territories, Poole 1994), man is the proximate influence on lynx density throughout most of the lynx's range (Parker et al. 1983, Ward and Krebs 1985; see Koehler and Aubry 1994 for review). Evidence that this mortality is not always compensatory is suggested by low lynx densities after heavy harvests during a period of high snowshoe hare densities on the Kenai Peninsula (Bailey et al. 1986) and dampened amplitudes of peak lynx abundances in Alberta (Todd 1985). For the immediate future, the threat of over-trapping has been released throughout the lynx's southern range due to moratoriums (WA, UT, MI, ND, OR, ME, NH, WI, VT, MN, CO) and reduced quotas (ID, MT).

Ultimately, lynx density is probably a function of habitat quality and quantity, as suggested by the correlation of fire occurrence to peaks in lynx fur harvests (Fox 1978) and the comparison of southern vs. northern snowshoe hare and lynx demography (Chapt. 2). However, one of the least studied aspects of lynx ecology is lynx habitat relationships. Most lynx research has addressed

⁴In Canada, pelt prices jumped from \$38 in 1971-72 to \$216 in 1975-76 (Brand and Keith 1979), increasing to \$225-355 in the early 1980's, with the best pelts selling for \$1,000 or more (Todd 1985). Fed. Register (1994) reported that pelt prices were \$12.00 a piece in 1977.

population dynamics in relation to fluctuating prey availability rather than habitat associations, with the motivation that understanding lynx density patterns through time should enable biologists to manage this valuable fur resource at a sustainable level. As once remote lynx habitat becomes developed, mined, and logged, the need to clarify lynx habitat associations and the effects of land management activities on lynx persistence and density has become imperative. The status of lynx may only be effectively ascertained and recovery strategies developed after these relationships are clarified.

1.3 DNR's Role in Lynx Habitat Management

Instead of adopting a species-specific critical habitat rule (i.e. WAC-222-16-080 [1]) in response to the listing of lynx as a state-threatened species, the Washington Forest Practices Board (February 9, 1994) recommended creation of a "special wildlife management plan" (WAC-222-16-080 [2]), coordinated with and approved by WDFW. As one of the three major non-federal landowners within primary lynx range, DNR undertook development of this lynx habitat management plan. Boise Cascade, Inc. and Plum Creek Timber Co. (lands now owned by Stimson Lumber Co.) were the other landowners involved.

In addition to the Washington Forest Practices Board agreement, internal policies encourage management of lynx habitat on land managed by DNR. Specifically, Forest Resource Plan Policies 20, 22, and 23 (DNR 1992) direct DNR to establish Riparian Management Zones, provide upland wildlife habitat, and "participate in efforts to recover and restore endangered and threatened species."

DNR will contribute to the future of Washington's lynx population by improving habitat conditions and/or lessening probabilities for adverse effects on the habitat it manages within the legal obligations specified in the Trust Mandate (DNR 1992). DNR manages 5% of the primary lynx habitat in Washington, including some land in each of the six Lynx Management Zones recognized by WDFW (WDW 1993, Fig. 2). Most (75%) of the lynx habitat managed by DNR is within the Okanogan Lynx Management Zone, including 20-30% of the area occupied by lynx during the mid-1980's lynx studies (Brittall et al. 1989, Koehler 1990a) in northcentral Washington.

DNR is committed to following a lynx habitat management plan until the lynx is de-listed, or 80 years, whichever is shorter. This initial version of DNR's Lynx Habitat Management Plan will be revised and updated as more is learned about lynx habitat relationships (6.2).

1.4 Planning Considerations

1.4.1 Assumptions

The urgency of conservation efforts that accompanies threatened and endangered species recovery often forces biologists and land managers to make decisions without statistically rigorous data to guide them. All too often, an educated guess becomes an accepted policy before it is tested. This may not only prevent important relationships from being recognized in the data collected, but it may also be difficult to change the policy once it has already been incorporated into management plans. With most endangered species, there is little time for misdirection. For these reasons, management plans should take an experimental approach with careful planned actions centered on hypotheses that can be modified, tested, and refined (Walters 1986, Murphy and Noon 1992). Biologists aware of the uncertainties involved should relentlessly remind interested parties of the hypothetical nature of their endeavors and clearly identify their assumptions.

The strategies within this document are extensions of current hypotheses of lynx ecology, as detailed in Chapter 2. The information is provided so that future biologists and land managers can more easily adapt to scenarios overlooked by the plan and replace errant strategies as more is learned about the habitat associations and status of lynx. Meanwhile, general considerations for the conservation of lynx based on Thomas et al. (1990; northern spotted owl), as presented by Weaver (1993), were adopted in the development of this document (Table 1). It is presumed that a plan based on these considerations will contribute to the continued persistence of lynx in Washington.

Table 1: Assumptions adopted in DNR's Lynx Habitat Management Plan.

- a. Species that are well-distributed across their historic range are more persistent than species confined to small portions of their range.
 - b. Population persistence increases with the number and size of sub-populations and the size of habitat blocks.
 - c. Blocks of contiguous habitat in close proximity promote a higher probability of persistence than dispersed blocks of fragmented habitat.
 - d. Population persistence increases when blocks of habitat are interconnected through linkages of suitable habitat.
 - e. The persistence of exploited populations increases with a well-distributed network of refuges or safety nets.
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1.4.2 Plan Scales

DNR's lynx habitat management strategy employs a multi-scaled structure for lynx habitat management (Table 2), modeled after the "Hierarchical Approach" recommended by the interagency Western Forest Carnivore Committee (1994). This nested structure reflects the difficulty of managing habitat for large terrestrial carnivores. The needs of individual lynx, as well as of the species in general, cover many spatial scales. For example, lynx home ranges as small as 2.7 mi² (7 km²) were recorded in an untrapped area in the Yukon, reflecting a relatively small scale. In the same area, 17 lynx traveled >62.2 miles (100 km), with 11 recorded at distances of 311-684 miles (500-1,100 km) from their original collaring locations, reflecting an immense scale of potential habitat use (n=161, Slough 1995). These locations represent collared lynx that were trapped, indicating that they might have even traveled farther if their journeys were not so fatally interrupted. Therefore, managing lynx habitat requires land managers to consider not only the habitat within their jurisdiction, but also the larger context in which their land is situated. The relationships of this plan's scales are diagrammed in Fig. 3.

Management ratios and guidelines in this plan focus on the Lynx Analysis Unit level (Table 2), with the small-scaled goal of maintaining the integrity of habitat regularly used by individual lynx or family groups. The LAU's are generally large enough to encompass the median lynx home ranges reported for lynx in northcentral Washington (Table 3; Brittell et al. 1989, Koehler 1990a). The larger LAU's may be capable of supporting more than one lynx. It is important to emphasize that the LAU is simply a frame to monitor change on the landscape through time. As forests grow, lynx will undoubtedly shift their habitat use without regard to LAU boundaries. Meanwhile, LAU boundaries stratify landscapes into planning units which are then encompassed by two higher spatial scales to incorporate habitat connectivity from a broader perspective (Fig. 3).

In each of the following sections, the four scales employed in this plan are described, objectives are identified, and management strategies are outlined. Scales within the plan were chosen to facilitate 1) the ecological attributes of habitat within the lynx range, 2) the biological needs of lynx, and 3) coordination of lynx habitat management efforts with other state and federal agencies and British Columbia.

Table 2: The hierarchical structure of DNR's Lynx Habitat Management Plan.

Scale	Source/Size	Description	Objective	Management Strategy
Ecoprovince and Ecodivision	Demarchi 1992 and USFS 1994	derived from climatic processes and habitat types	encourage genetic integrity at the species level	1) prevent bottlenecks between B.C. and WA by limiting shape and size of non-habitat along the border 2) maintain major routes of dispersal between B.C. and WA
Lynx Management Zone	WDW 1993 6.6-2,885 mi ²	estimated from sightings, trapping records, habitat types, and elevation	maintain connectivity between sub-populations (within Washington)	1) maintain dispersal routes between and within zones 2) arrange harvest activities that result in non-forest patches among watersheds so that connectivity is maintained within each zone
Lynx Analysis Unit (LAU)	WDFW GIS data (1995) 6.6-79.7 mi ²	delineated by Watershed Administrative Unit (WAU) and ownership boundaries	maintain connectivity between and integrity within home ranges used by individuals and/or family groups (within sub-populations)	1) provide a diversity of successional stages within each analysis unit 2) connect denning sites and foraging sites with forested cover without isolating them with open areas
Small Ecosystem/ Ecological Community	WA Forest Landscape Management Project 20 - 400 acres	individual stands of similar vegetation, age, and structure	maintain the integrity of requisite habitat types within individual home ranges	1) prolong the persistence of snowshoe hare habitat 2) retain coarse woody debris for denning sites

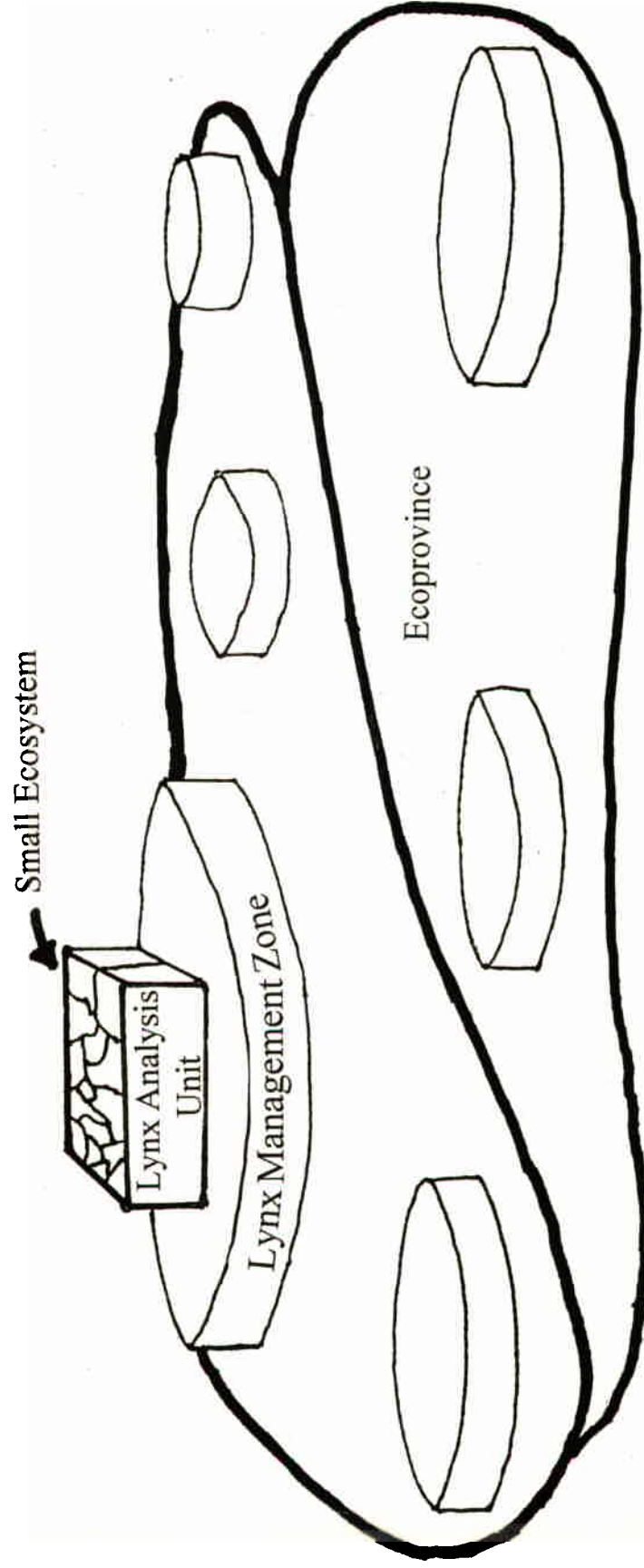


Figure 3: The hierarchical relationship of the four scales used in the Washington Department of Natural Resources Lynx Management Plan.

Table 3: Relative sizes of LAU's and lynx home ranges in Washington.

	LAU	Female Home Range*	Male Home Range*
n	29	9	13
median	31.6 mi ² (82 km ²)	14 mi ² (36 km ²)	21 mi ² (54 km ²)
range	6.6 - 79.7 mi ² (17 - 206 km ²)	3.2 - 33.9 mi ² (8.3 - 87.8 km ²)	9.6 - 38.2 mi ² (14.2 - 99.0 km ²)

*minimum convex polygon method, Brittell et al. 1989, Koehler 1990a

1.4.2.1 Ecoprovinces and Ecodivisions

Following the recent U.S. Forest Service [USFS] publication "The Scientific Basis for Conserving Forest Carnivores: American Marten, Fisher, Lynx, and Wolverine in the Western U.S." (Ruggiero et al. 1994), the largest scales considered in this strategy were "ecodivisions" and "ecoprovinces" (Table 2; Demarchi and USFS 1994). Use of these common scales, developed by USFS and British Columbia's Ministry of Environment, Lands, and Parks, facilitates the coordination of lynx management efforts on DNR-managed lands with other state, federal, and Canadian agencies. Ecodivisions and ecoprovinces are based on macroclimatic processes, or, "the relatively permanent atmospheric and geographical factors that govern the general nature of specific climates" (Demarchi and USFS 1994:153). Each ecodivision is usually subdivided by more than one ecoprovince. Within the primary lynx range of Washington, the Semi-Arid Steppe Highlands Ecodivision of the eastern Cascades and the Humid Continental Highlands Ecodivision of northeastern Washington are exclusively represented by the Shining Mountains Ecoprovince and Thompson-Okanogan Ecoprovince, respectively (Table 4, Fig. 4).

According to traditional biogeographic theory, lynx in both ecoprovinces of Washington are especially susceptible to extinction due to their peninsular distribution (Weaver 1993). The peninsular shape arises naturally from the distribution of habitats that lynx prefer. Boreal habitat and climate conditions at southern latitudes are restricted to increasingly higher elevations. Because these narrow mountain ranges have north-south orientations, lynx distribution maps depict peninsular ranges separated by lower elevation, less suitable habitat (Fig. 2).

Peninsular populations are notoriously vulnerable to extinction due to their degree of physical and genetic isolation (Taylor and Regal 1978). The tip of an extremely isolated peninsula may function like an island, whose ability to support a population is often dependent on size ("area

Table 4: Locations, landforms, and climates of ecodivisions and ecoprovinces within lynx range of Washington.*

ECODIVISION		HUMID CONTINENTAL HIGHLANDS	SEMI-ARID STEPPE HIGHLANDS
Location		central interior of British Columbia, east of the Coast Mountains to the Interior Plains, extending south into northeastern Washington, northern Idaho, and northwestern Montana	directly east of the Coast Mountains and Cascade Ranges of southern British Columbia, Washington and northern Oregon
Landforms		mountains, plains, basins	basins, plateaus, mountains
Climate	summer	warm and dry	warm to hot, and dry
	winter	cold-Arctic	cold, dry; not usually affected by Arctic air
	precipitation	from Pacific air mass with some additional moisture from heating of wetlands, streams, and lakes	from Pacific air mass, but reduced quantities due to the rainshadow created by the western mountains; peak precipitation is early in the growing season
ECOPROVINCE		Shining Mountains	Thompson-Okanogan Highlands
Landforms		includes the following physiographic systems east of the western highlands: Columbia mountains, Southern Rocky Mountain Trench, Rocky Mountain Foothills of Alberta and Montana, Border Ranges of the northern Rockies (MT), and mountains of the Idaho panhandle	east of Cascade Mountains to the west margin of the Shushap Highlands, south to Lake Chelan, including the Thompson Plateau, Pavillion Ranges, and Okanogan Highlands
Climate	summer	intense surface heating causes updrafts in mountains	irruptions of hot and dry air from the Great Basin contribute to arid conditions
	winter	outbreaks of Arctic air travel through the Rocky Mountain Trench toward the Rocky Mountain Foothills and eastern Rockies	frequent irruptions of cold, dense Arctic air due to the lack of a barrier between the interior British Columbian Plateaus and the region; outbreaks are less frequent than on the northern plateaus
	precipitation	air passing from the west loses moisture successively as it passes the western Columbia mountains, Bitterroot Ranges, and Rocky Mountains	level air flow from the Pacific results in reduced precipitation, most of the Pacific air loses moisture on the west slope of the coastal mountains before reaching here; some precipitation from surface heating of lakes and streams

*adapted from Demarchi and USFS (1994)

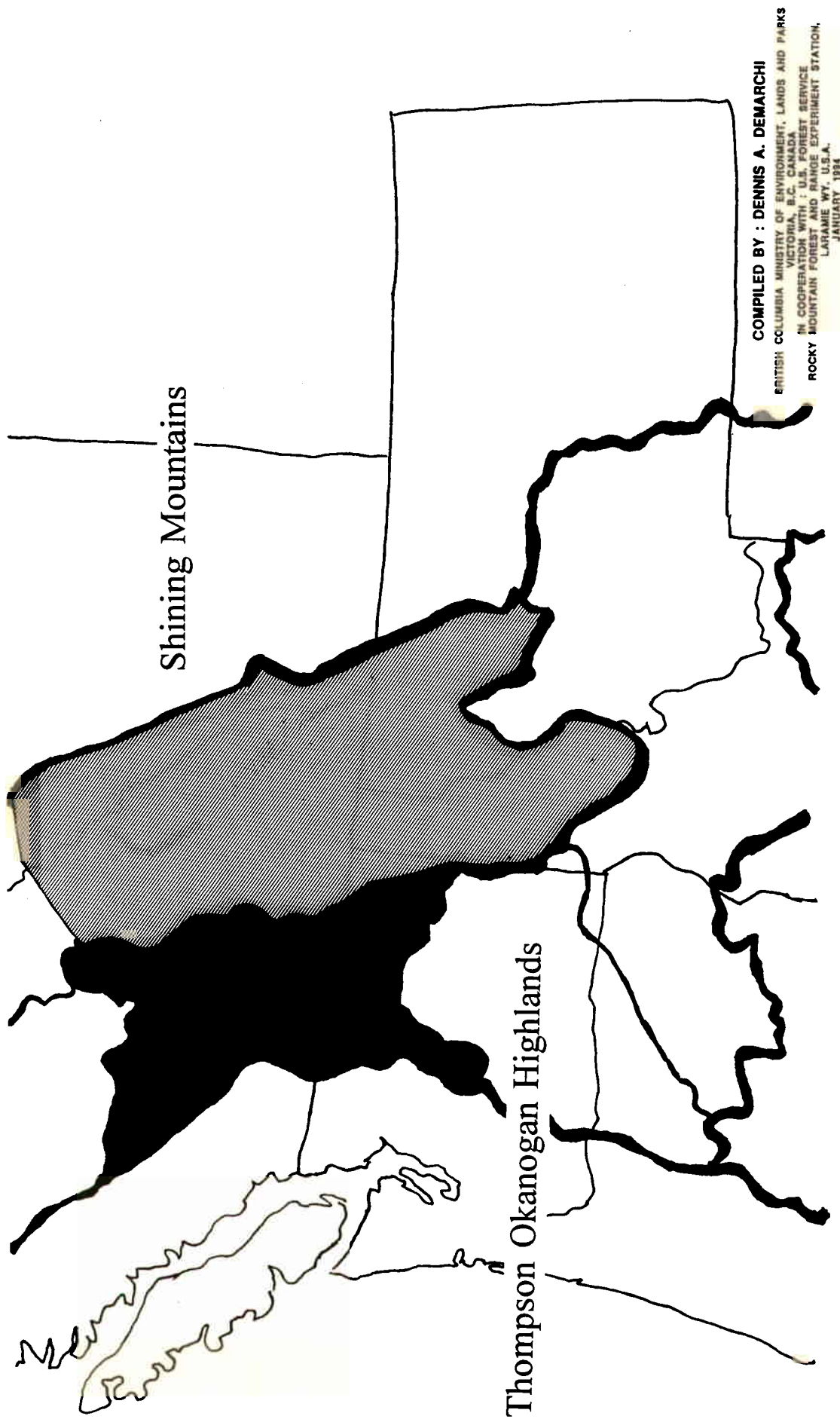


Figure 4: Ecoprovinces of northeastern Washington (Demarchi and U.S.F.S. 1994).

effect"). If the resources of a species are depleted on a mainland, individuals may emigrate to another part of the mainland to find replacement resources. On islands or isolated habitats where such movements are impeded, mortality may ensue. Resource depletion is especially a problem among habitat or prey specialists, like the lynx, which may be unable to persist on alternative prey (Poole 1994). Immigration to islands or isolated areas may also be restricted, increasing the likelihood of inbreeding problems and severity of disease or parasite outbreaks, should they be present. The dispersion of suitable habitat associated with mountainous terrain may also influence species persistence. Constriction of a species' occupied range under these conditions may amplify its vulnerability to extinction. For a more detailed summary of "The Process and Factors of Extirpation" in reference to lynx, see Weaver (1993).

From the distribution map (Fig. 1), it appears that the Washington lynx habitat contributes to the species' integrity broadening the habitat "peninsula" that extends into the conterminous United States. Maintenance of this habitat connection between the northern Canadian populations and southern populations may decrease the probability that the southern populations will succumb to random stochastic events leading to extinction. Future research may reveal the degree to which the persistence of Washington populations are dependent on the connection to Canada, and what role the Washington habitat plays as a link between north and south.

To address considerations a) and d) of Table 1 and to encourage genetic integrity at the species level (Table 2), the habitat management strategy at this scale is to 1) prevent bottlenecks between British Columbia and Washington by minimizing the size of openings created by harvest activities at the longitudinal border, and 2) maintain major lynx travel routes between Washington and British Columbia.

1.4.2.2 Lynx Management Zones

The second scale employed utilizes the six zones of primary lynx range identified by WDFW (Table 2, Fig. 2). These zones were refined from those originally identified by Brittell et al. (1989:83) and reflect surveys, field notes, sightings, trapping records and reports, elevation, and vegetative communities. Although all are considered primary habitat, each zone has a slightly different history and potential as lynx habitat (WDW 1993). Accessibility, trapping history, past forest harvest activities, fire suppression practices, size of current lynx population, total area, vegetative communities, and landscape heterogeneity are some of the variables contributing to the differences in potential between zones. Descriptions of each zone are detailed in the next chapter.

Addressing considerations b), d) and e) of Table 1 and maintaining connectivity between sub-populations (within Washington, Table 2), the habitat management strategy at this scale is to 1) maintain dispersal routes between (i.e. east-west travel routes) and within zones (i.e. north-south

travel routes), and 2) arrange harvest activities that result in non-forest patches or other dispersal barriers among watersheds so that connectivity is maintained within each zone.

1.4.2.3 Lynx Analysis Units

To evaluate current and potential habitat conditions and distribute within-zone management action, LAU boundaries were employed to stratify the Lynx Management Zones (Table 2). LAU's were delineated by WDFW based on Watershed Administrative Unit [WAU] boundaries (WDFW, pers. commun.). Also, lynx home ranges in northcentral Washington appear to correspond with drainage boundaries (Koehler and Aubry 1994). Parker (1981) likewise concluded that lakes and streams contribute to the definition of home range boundaries of lynx on Cape Breton Island, Nova Scotia. The LAU system was selected to facilitate interaction with other agencies and industries.

Descriptions of LAU's that contain DNR-managed land are detailed in the next chapter. Habitat potential and management recommendations are discussed in blocks of ownership where adjacent lands are dissected by multiple LAU boundaries.

Addressing considerations c), d) and e) of Table 1 and maintaining connectivity between and the integrity of home ranges used by individuals and/or family groups (Table 2), the habitat management strategy at the LAU scale is therefore to 1) provide a mosaic of successional stages within each analysis unit, and 2) connect denning and forage areas while avoiding isolation of either with open areas.

1.4.2.4 Small Ecosystems/Ecological Communities

Activities at this scale are designed to maintain the integrity of requisite habitat elements within individual home ranges (Table 2). The habitat management strategies are to 1) prolong the use of stands by snowshoe hares, and 2) to retain coarse woody debris for denning sites.

Chapter 2:

PATTERNS OF HABITAT USE BY LYNX AND SNOWSHOE HARE

This chapter familiarizes the reader with what is known and unknown about lynx and hare habitat relationships. Topics covered range from stand to landscape scales, forming the foundation from which the lynx management plan was derived. In the first section, lynx use of forests is discussed. Next, forested habitats are examined from the perspective of snowshoe hare. The last two sections consider lynx and snowshoe hare habitat relationships at landscape scales, in terms of prey and habitat availability through time.

2.1 Lynx Habitat Relationships

2.2 The Perspective of Prey: Predation and Snowshoe Hare Habitat Relationships

2.3 Landscape Patterns and Processes and Snowshoe Hare Habitat Relationships

2.4 The Effect of Landscape Level Snowshoe Hare Dynamics on Lynx

2.1 Lynx Habitat Relationships

Lynx encounter many types of forests in many structural stages throughout their trans-North American distribution, and undoubtedly alter their use of habitat as the influences of climate, topography, competition, exploitation, and predation change among landscapes. For these reasons, it is not advisable to directly transfer the conclusions from one study to another in a different location (Skalski and Robson 1992). However, results of studies from different locations can be used to formulate hypotheses and direct future research in other locations. The following sections review the information used to develop the lynx habitat management guidelines and ratios of the next chapter.

2.1.1 Midsuccessional Forests⁵

The most undisputed habitat association in lynx natural history is the tie between lynx and midsuccessional forests. The literature is nearly unanimous in supporting this relationship, offering examples of lynx establishing nearly their entire home ranges within such habitat, regardless of latitude or season (i.e. winter tracking vs. year round telemetry): an area actively used by two lynx in Newfoundland almost exactly coincided with the boundary of a 10-20 yr. old forest (Saunders 1961), 90% (n=29) of the relocations of two lynx were within densely stocked stands in Montana (Koehler et al. 1979), 87% (n=391) of the relocations of 11 lynx were in a 31 yr. old burn on the Kenai Peninsula in Alaska (Kesterson 1988), lynx were relocated in regenerating lodgepole pine more than expected ($p < 0.001$) in the Yukon (Major 1989), lynx tracks were most abundant in sites logged 20-30 years previous to study in Ontario (Thompson et al. 1989), and 98% (n=240) of lynx tracks observed on snow tracking surveys in central Interior Alaska were located in a 25 yr. old burn (Johnson et al. 1995). Some of the highest lynx densities recorded (50 lynx/100 km² or 2 lynx/3mi²) occurred in a ~30 yr. old burn in the Yukon (Slough 1995, Breitenmoser et al. 1993). The primary reason for the tight association between lynx and midsuccessional forests is that this habitat contains the highest densities of snowshoe hare, the staple prey of lynx.

⁵Midsuccessional forests in this document are those resembling a 20-40 year old forest that has regenerated after a low to moderate intensity burn (e.g. 20-30 year old stands, Thompson et al. 1989). The forests are characterized by high vertical and horizontal vegetative cover as the result of high stem densities, with average tree heights of 7-20 feet (2-6m) and crown closure of 75-80% (e.g. Parker 1981).

2.1.2 Mature Forests: Preference or Avoidance?

Lynx are also associated with mature forests,⁶ but this relationship is not as clearly defined as the one between lynx and midsuccessional forests. Sometimes mature forests are used in proportion to their availability (Brittall et al. 1989, Parker et al. 1983, Murray et al. 1994), sometimes they are preferred (Parker 1981, Major 1989, Koehler 1990a, Staples 1995), and sometimes they are avoided (Parker 1981, Kesterson 1988, Thompson et al. 1989, Staples 1995). The potential relationship between lynx and mature forest might be clarified if there were standard methods to describe the vegetative quality of study sites for comparison. For example, "mature forests" can contain low understories of shrubs or regenerating trees that are dense enough to support snowshoe hares in numbers similar to midsuccessional forests (2.3.6.2). Other differences in vegetative structure that may influence the use of mature forests by lynx include debris for den sites (2.1.3).

Context is another important variable that may influence habitat preference results. Wildland fires often leave unburned inclusions, patches, or stringers. In time, these areas are often used by lynx (Koehler et al. 1979, Kesterson 1988, Staples 1995), because they conveniently juxtapose prey supply with denning sites. It may also be easier for lynx to catch hares in these areas, which are more open than the regenerating forests (Major 1989, Staples 1995; 2.3.6.3 and 2.2.2.3). Therefore, when mature forest is reported as a component of lynx home ranges, "mature forest" may actually be referring to unburned remnants rather than the traditional contiguous stands of mature forest that first come to mind (but see Murray 1991).

Perhaps because habitat associations were not the primary focus of most previous lynx research, there is a lack of clearly defined terminology used to describe habitats and/or management activities within study areas. Researchers may measure different habitat characteristics, employ different methods to measure similar characteristics, use different analysis procedures, and/or sample different proportions of their study area using different numbers and sizes of plots, which makes comparisons across studies unreliable. Vegetation sampling can be especially problematic in studies of habitat use by larger terrestrial carnivores due the large area encompassed by home ranges.

Lastly, GIS has only recently been applied to wildlife studies, so little quantification of habitat types is available. In those studies that address availability, preference for mature forests may be the result of how availability was defined (Johnson 1980). For example, including large areas of habitat not regularly used by lynx (open areas, see below) may indicate preference for mature

⁶"Mature forests" in this context refer to forests older than midsuccessional forests, a general definition to account for the many ways the term has been presented in the lynx literature.

forests, while restricting the definition of "available" habitat to forested areas only may show that forested stands of various ages and structures may be used equivalently.

The above problems complicate comparisons and analysis among studies. The lack of consistency suggests that further investigation of mature forest use by lynx is warranted.

2.1.3 Mature Forests: Denning Areas

When significant use of mature forests by lynx is detected, a commonly cited reason is for denning (Table 5). However, structure, in the form of log piles (i.e. deadfall, windfall, jack-strawed woody debris, etc.), rocks, root tangles, shrub thickets, or similarly dense vegetation (subalpine fir; B. Slough, Yukon Dep. Renewable Resour., pers. commun.) is the common denominator of known denning areas. Such structures may therefore be the critical components of denning areas, rather than the mature state of the forest, as indicated by the observation of successful lynx dens in slash piles within old burns and shrub thickets in riparian and subalpine areas (G. Mowat, Lethbridge Community Coll., pers. commun.; Slough and Ward 1990). Of all structures used as dens by lynx, windblown piles of jack-strawed logs seem to be most commonly used. For example, 35/40 dens were located in such structure in the Yukon (B. Slough, *in prep.*).

Discrepancies concerning lynx preference for mature forests might result from differences in availability of denning structure among study areas. For example, in northcentral Washington (Koehler 1990a), denning structure may be more consistently available within older stands on mesic sites due to the fire regime. The hypothesis is that xeric conditions on neighboring sites lead to smaller diameter, stressed trees that are more readily consumed by frequent, intense fires. Thus, denning sites would be relegated to fire-resistant stands. Insect activity and wind patterns (producing blowdowns) also likely influence den site availability in northcentral Washington.

Similar to denning structure, the availability of preferred climate conditions may also be unevenly distributed in the landscape. A hypothesis for the southern lynx range related to this is that aspect and forest maturity influence selection of denning habitat (Koehler 1990a) because the cool, moist climate of older stands on northern slopes may more closely emulate denning conditions within the boreal forest.

In any case, lack of denning habitat or mature forests have not yet been cited as reasons for low recruitment in lynx. Instead, the success of reproduction is linked to the abundance of snowshoe hare (Nellis et al. 1972, Brand et al. 1976, O'Conner 1984, Ward and Krebs 1985, Poole 1994). As stated by T. Bailey (Kenai Natl. Wildl. Ref., pers. commun.), "more important (than specific habitat types or their availability for denning) appears to be the proximity of such stands to high prey densities."

Table 5: Qualitative descriptions of denning sites at various locations within lynx range.

Wisconsin

(Jackson 1961:400)

"The den where the young are reared is in a hollow tree, stump, or log, and sometimes under fallen timber. The nest consists of leaves, bark, and similar vegetative matter pawed and trampled into form by the parent."

Interior Alaska

(Berrie 1973, abstract from Butts 1992)

"Three apparent natal dens were found, two in spruce blow down situations and one in 'a tangle of washed up spruce roots' beside a creek."

(Stephenson 1986, in Hatler 1988)

A suspected den site was characterized by "mixed mature spruce and birch where numerous windfalls were present."

Kenai Peninsula, Alaska

(Bailey 1992, letter to Russ Paul)

"Denning habitat is almost always mature forest stands with many downed logs, and windblown trees and root systems... The ideal den site is a small stand of mature forest surrounded by earlier successional stage forest with high hare densities."

Okanogan, Washington

(Koehler 1990a)

Two females used denning sites "characterized as mature (>250 yrs old) stands with an overstory of Engelmann spruce, subalpine fir, and lodgepole pine. All denning sites were located on north-northeast aspects, with an average of 40 downfall logs/50m. Kittens were observed using the down logs for escape cover."

(Koehler and Brittell 1990:12)

"Downed logs and stumps provide cover for kittens and may be the most important component of denning habitat."

Yukon

(B. Slough, 1992 letter on file)

"Contrary to what Gary Koehler found in Washington and Montana, old growth was not a requisite; rather, dense cover in any habitat was utilized. (Because) our study area was burned, most lynx dens were under deadfall in immature lodgepole pine, white spruce or subalpine fir regeneration."

(M. O'Donoghue, Univ. British Columbia, pers. commun.)

"Dens may be found in all forest types as long as there is adequate cover (blowdowns, deadfall)."

Northcentral British Columbia

(Hazelwood, in Hatler 1988)

One den site was "located at the edge of a 6-8 year old clear-cut near Houston. Logging debris had been pushed into a windrow along the forest edge, and there was extensive blowdown on top of that."

2.1.4 Mature Forests: an Alternative to Open Areas

Many lynx researchers hypothesize that mature forests are important to lynx, perhaps outside of denning (e.g. Parker et al. 1983, Johnson et al. 1995, Staples 1995), perhaps for habitat in which to travel between prey areas (Parker 1981). An examination of the disassociation between lynx and open areas,⁷ a well recognized and reported relationship (Koehler et al. 1979, Parker et al. 1983, Murray et al. 1994, Poole 1994), may help clarify this possibility. Among the many reasons a lynx might avoid open areas, and thereby prefer forested areas, are the following: 1) to find favorable thermoregulatory conditions (e.g. cool and moist over hot and arid conditions in the summer, warm and calm over cold and windy in the winter), 2) to avoid predation, and/or, 3) to increase contact with prey.

2.1.4.1 Thermoregulatory Conditions

Are lynx avoiding open areas or choosing forested areas for thermoregulatory benefits? Increased use of mature forests in summer was reported on the Kenai Peninsula, Alaska (Staples 1995) and on Cape Breton Island, Nova Scotia (Parker et al. 1983), but the authors suggested that the switch reflected a decreased dependence on snowshoe hare in the snow-free season, rather than thermoregulatory benefits. Thermoregulatory influence on habitat selection might be most easily detected in southern areas of lynx range, where there is sharper distinction among available habitats and climates due to the effects of topography, altitude, and latitude. Kittens may be more susceptible to physiological constraints associated with habitat type due to their developing state. However, both avoidance of (Washington, Koehler 1990a) and preference for (Montana, Koehler et al. 1979) xeric habitats by lynx in southern areas has been reported. Instead of climate, the authors of these studies referred to the importance of prey availability in determining habitat use by lynx. Although such qualitative comparison does not suffice for determining how physiological constraints may influence lynx habitat selection, it reaffirms the prominent role of prey in determining habitat use by lynx in the areas studied.

⁷"Avoidance" used here implies *general* avoidance. Lynx sometimes do cross open areas (most often <328 feet (100m) wide; Koehler and Brittell 1990; B. Slough, Yukon Dep. Renewable Resour., pers. commun.; Staples 1995) or sun themselves in them (Parker 1981), but most of the time they avoid them (e.g. Halfpenny and Biesiot 1986). For example, lynx crossed a lake 0.6 mile (1km) wide in the Yukon, but most often walked around it (G. Mowat, Lethbridge Community Coll., pers. commun.). In Alaska, 0.8% of lynx tracks crossed open habitats despite these habitats covering 20% of the study area (Staples 1995).

2.1.4.2 Predator vs. Predator Interaction

Predation on adult lynx in North America has rarely been recorded in the literature, leading authors to conclude that lynx have few natural enemies (Jackson 1961, Quinn and Parker 1987).⁸ If this were true, there would be little impetus for lynx to evolve selection for forested habitat types out of fear of becoming prey in open areas. However, the reason for so few historical records of predated lynx may be that lynx are adept at escaping or avoiding potential predators.

Behavioral clues suggesting that lynx are hesitant to cross open areas have been interpreted from tracks left in snow (Staples 1995:63): "lynx sat long enough on the edges of open areas to change position and orientation of their hind legs three or more times." In the forest, lynx likely avoid some predation by climbing trees (Staples et al. 1995; B. Slough, Yukon Dep. Renewable Resour., pers. commun.). After examining accounts of human/lynx interactions, Staples et al. (1995) postulated that the ability of lynx to escape by tree climbing has resulted in extraordinary confidence: unlike coyotes that fled within a distance of 100-200 yards from people (67%, n=33), lynx were curious or indifferent to most encounters (89%, n=92). Other tales of lynx following people through wild areas or otherwise being "curious" may also support this conclusion (Jackson 1961), but such behavior may be motivated by starvation rather than "confidence."

The rarity of observed predation may result from limited opportunities to observe such events. As more studies on lynx are undertaken, there is increasing evidence of periodic intraguild predation associated with lows in the snowshoe hare cycle (Polis et al. 1989, O'Donoghue et al. 1995). With an adequate prey source, two predators can occupy overlapping areas at the same time (coyotes, bobcats, and mountain beaver in Oregon, Witmer and DeCalesta 1986). As the ratio of prey to predator declines, predator vs. predator interactions may become more common (O'Donoghue et al. 1995). Declines in abundance of many species correlate with the decline of hares: coyote, fisher, red fox, lynx, marten, mink, muskrat, skunk, wolf, and wolverine (Canada, Bulmer 1974); marten, red squirrel, red fox, lynx, ermine (Ontario, Thompson et al. 1989); coyote, weasels, sciurids, porcupine, and skunk (Alberta, Todd et al. 1981, Keith and Cary 1991).

Documented predation events involving lynx include lynx killed by other lynx (Elsey 1954, O'Donoghue et al. 1995, Slough 1995, Poole 1995), cougar (Koehler et al. 1979), wolves (O'Donoghue et al. 1995, Staples et al. 1995, Staples 1995), and wolverines (Slough 1995).

⁸There is some evidence that predators influence lynx behavior in Asia. An apparent increase in wolf abundance was accompanied by a decrease in the abundance and distribution of European lynx in eastern Slovakia (Guggisberg 1975). Whether this was displacement or predation, the effect may also occur with lynx in North America where wolves still occur, especially considering that the North American species is smaller than its European counterpart. Likewise, a European lynx was also observed to move from a kill when a wolverine approached it (Guggisberg 1975).

Reported relationships between coyotes and lynx is contradictory: although there was at least one report of a lynx killed by a coyote (O'Donoghue et al. 1995), lynx on the Kenai Peninsula were not deterred by coyotes (Staples 1995). Some of the above events may have involved kittens or yearlings, which are certainly more vulnerable to predation than adults due to their size, physical development, and inexperience.

Thus it seems that there is a possibility that predation pressure may indeed encourage lynx to seek out mature forests for escape from other predators, especially at low prey densities. This suggests yet another way that prey density may influence lynx habitat selection. Given the low prey densities suspected in Washington (Koehler 1990b), predation pressure may indeed be a significant influence on lynx habitat use in Washington.

2.1.4.3 Rate of Prey Encounter

A third possible reason for the avoidance of open areas by lynx is that there is a lower probability that lynx may encounter and catch prey in such habitats than in mature forests. Although snowshoe hares use open habitats at least occasionally, they are most reliably found in areas with dense vegetation.

Lynx often require at least some amount of cover (vegetation, rock, or other debris) because their hunting techniques rely on close approaches (e.g. Bergerud 1983, Sunquist and Sunquist 1989). Like other felids (Ewer 1973), lynx are not fast on their feet over long distances (estimated 12 miles/hr or 19.3 km/hr, Jackson 1961). Although some chases have reached 150-300 feet (55-110m) (Parker 1981), lynx achieve greatest success by stalking close to their prey and pouncing on it after one or two bounds of six to ten feet (2-3m) (Nellis and Keith 1968, Guggisberg 1975, Parker et al. 1983, Murray and Boutin 1991, Major 1989). Lynx may also occasionally leap from a branch to seize prey (Saunders 1961, Guggisberg 1975). Overall, hunting success seems more dependent on hunting conditions (i.e. optimum cover for close hare encounters and snow for pursuit) than hare abundance (Nellis and Keith 1968, Parker et al. 1983). Lynx are more conspicuous in the open, and therefore not as likely to be successful in stalking prey.

Considering that hares may only be at high numbers for a few years out of their approximately ten year cycle, and that lynx may live up to 12 years (Jackson 1961; usually less, M. O'Donoghue, Univ. British Columbia, pers. commun.), lynx probably only have a few years (4-5, estimated by Brand et al. 1976) when there is enough prey to support successful recruitment. This implies that lynx are probably nutritionally deprived during the troughs between hare peaks. Therefore, while commuting between high quality prey sites, it would be beneficial to take the route offering the highest chance of encountering prey. For most years, the greatest opportunities would be found on routes through forested habitats. Tracking surveys confirm that lynx spend most of their active hours (early evening to early morning) searching for food (Saunders 1961)

and opportunistically take alternative prey while traveling (Parker et al. 1983). Also, lynx hunting success is related to the rate that lynx encounter hare, which increases with hare density (Brand et al. 1976).

Lastly, lynx family groups appear to travel in both open areas (Saunders 1963b) and open mature forests (Parker et al. 1983) using the same, single file (mother first) strategy. In midsuccessional habitat, the lynx family group travel strategy is to fan out and zig-zag (Saunders 1963, Parker et al. 1983, Major 1989). Both habitat types support relatively lower hare densities than midsuccessional forests or older forests with low, hare supporting understories (2.3.6.2). It is possible that the strategies are therefore related to the difference in cover available to secure lynx from predators. However, Parker et al. (1983) and Major (1989) report that the zig-zag strategy is used to flush prey. Single animals similarly use straight-line travel through low prey density areas and a zig-zag pattern where prey is present (Staples 1995).

Where and when hare density is low, opportunities for chance encounters with *alternative* prey provided by mature forests may be critical. A relatively high frequency of red squirrels (24%) in the diet of lynx was reported in northcentral Washington (Koehler 1990a). Correlating the high proportion of potential squirrel habitat in the study area (>80% mature forest) with relatively high availability of squirrels,⁹ this situation could have resulted from lynx taking squirrels opportunistically as they traveled between hare patches. Other studies have similarly referred to the importance of red squirrels to lynx survival during hare lows (Bailey et al. 1995, O'Donoghue and Hofer 1995, Staples 1995). Considering that it takes nearly seven red squirrels to equal the biomass of one snowshoe hare (Brand et al. 1976), it would generally not be energy efficient for lynx to hunt squirrels instead of hares. However, the frequency of red squirrels in lynx diets reached 75% during a hare low within a white spruce forest in the Yukon (M. O'Donoghue, Univ. British Columbia, pers. commun.). At this time, it was apparent that lynx were actively hunting squirrels rather than taking them opportunistically (M. O'Donoghue, Univ. British Columbia, pers. commun.). Relative availability of squirrels may therefore be an important variable in understanding the habitat needs of lynx, because starving lynx generally emigrate or die (Ward

⁹The habitat associations of red squirrels are another topic for future research. Whereas hare densities generally decline in mature forests (related to understory characteristics, Parker et al. 1983, Bailey et al. 1986 and Staples 1995, Koehler 1990b), red squirrels can reach similar densities in the 20-30 year old stands preferred by hares as older stands (Sullivan and Moses 1986, Thompson et al. 1989, Koehler et al. 1990). However, habitat quality may not be equivalent among stands of different ages (Sullivan and Moses 1986). Tree squirrels are food limited. Therefore, the best squirrel habitats should be mature forests where cone densities are generally higher and more reliable (Smith 1968, 1970; Rusch and Reeder 1978; Buchanan et al. 1990). However, the diet of red squirrels includes many other items, including berries, insects, nuts, and fungi (Dalquest 1948, Smith 1968), and even snowshoe hare (O'Donoghue 1994). These items may be readily available in younger forests in certain years (Thompson et al. 1989). As squirrel densities and habitat occupancy patterns vary with environmental fluctuations (Smith 1981), high quality habitats (mature forests) may become important sources of squirrels for recolonization (Buchanan et al. 1990).

and Krebs 1985, Poole 1994). Mature forests may also provide lynx with access to voles (Koehler et al. 1990), a possibly important alternative prey in the snow-free season (Staples 1995). Clearly, further research on the role of alternative prey in lynx diets will be needed to improve our understanding of lynx habitat relationships.

2.2 The Perspective of the Prey: Predation and Snowshoe Hare Habitat Relationships

2.2.1 Patterns According to Age Class

For snowshoe hares to persist, the habitats available must enable hares to 1) avoid being eaten long enough to 2) find enough browse so that they can 3) successfully reproduce. From the beginning, the nutritious (20% protein; Whittaker and Thomas 1983), numerous, and available-in-winter snowshoe hares must overcome the difficulties of being the prey of many species (Table 6). Predation is the main cause of adult mortality (Brand et al. 1975), although starvation may play an equal role during population highs (Boutin et al. 1986).

Many aspects of the hare's reproductive ecology reflect the influence of intense predation risk, such as the lack of nest building, precocial young, reduced suckling time, as well as initial patterns of habitat use (Graf and Sinclair 1987, O'Donoghue 1991). One to seven days after birth, juvenile snowshoe hares leave the birth site and find shelter within the female's home range (Rongstad and Tester 1971, O'Donoghue 1991 and references therein, O'Donoghue and Bergman 1992). The dispersion of litter mates reduces the risk that an entire litter will be discovered by a predator at one time. Predation risk also appears to be reduced in the hare's nursing strategy: the female returns to the birth site once an evening for 5-10 minutes of nursing (decreasing mean time as the young mature, increasing with season; Rongstad and Tester 1971, Graf and Sinclair 1987, Martinet and Demarne 1984, O'Donoghue 1991). Newly born hares are able to suck 10% of their body weight in highly concentrated milk in 5 minutes (European hares, Martinet and Demarne 1984), also reducing the potential to expose an entire litter to predation.

For approximately 10-12 days, juvenile hares remain relatively motionless in their hiding spots, and are easily caught by hand (O'Donoghue 1991). Therefore, juvenile hares rely on concealed hiding cover and cryptic coloration to avoid predation (Adams 1959, O'Farrell 1965, O'Donoghue 1991). Cover is sought under shrubs, clumps of grass or herbs, logs, or in dead falls (O'Donoghue 1991). In the Yukon, 70% of early juvenile mortality occurred during the first 5 days after birth, and 51% of the litters had no known survivors after 14 days (O'Donoghue 1994). Small mammalian predators such as red squirrels and Arctic ground squirrels were the proximate cause of mortality during this time.

Table 6: Potential predators of the snowshoe hare.

Predator	Reference
lynx	O'Farrell 1965, see Koehler & Aubry 1994
coyote	Todd et al. 1981, Litvaitis & Harrison 1989
great horned owl	Adams 1959, Boutin et al. 1986, Sievert & Keith 1985
bobcat	Litvaitis & Harrison 1989, Theberge & Wedeles 1989
fisher	Powell 1981
goshawk	O'Farrell 1965, Reynolds & Meslow 1984
great grey owl	Earhart and Johnson 1970
wolverine	Rausch & Pearson 1972; Banci & Harestad 1988, 1990
American marten	Bateman 1986, Thompson & Colgan 1994
northern hawk owl	Rohner et al. 1995
red fox	Theberge & Wedeles 1989
barred owl	Morse 1939, Sievert & Keith 1985
golden eagle	Boutin et al. 1986
gray wolf	Fuller 1989, Boutin et al. 1986
raven	Morse 1939
long-tailed weasel	Dalquest 1948, Sievert & Keith 1985
snowy owl	Keith et al. 1977
rough-legged hawk	Keith et al. 1977
red-tailed hawk	McInville & Keith 1974
cougar	Anderson 1983
mink	Adams 1959, Sievert & Keith 1985
human	Dodds & Thurber 1965
feral dog	O'Farrell 1965
Arctic ground squirrel	O'Donoghue 1994
red squirrel	O'Donoghue 1994
gray jay	Graf & Sinclair 1987
short-tailed shrew	Rongstad 1965

Adult hares also rely on cryptic coloration and cover to avoid being detected by predators, but employ bursts of speed (up to 27 miles or 17 km per hour, Banfield 1974) and agile turns to escape into cover once detected (O'Farrell 1965). For example, a lynx will abandon a chase if the prey isn't captured after an average of 6-8 bounds (Nellis and Keith 1968, Murray and Boutin 1991) or about 25 feet (7.7m) (Major 1989). As summarized by Major (1989), the hare's initial response is to flee into cover. If the lynx gets between the cover and the hare, the lynx's probability of success increases.

2.2.2 Patterns in Response to the Ratio of Predators to Prey

The importance of cover to snowshoe hares can change according to the ratio of predators to prey. Strongly cyclic populations successfully exploit open habitat during peaks of hare abundance and retreat into dense vegetative thickets, or, "refugia," during population lows and under intense predation pressure (Keith 1966, Keith and Windberg 1978, Wolff 1980, Hik 1995). Specifically, hares at cyclic lows abandoned 72% (Keith 1966) and 87% (Keith and Windberg 1978) of habitats occupied during population highs in Alberta, and 90% of once occupied areas in Interior Alaska (Wolff 1980). Although dramatic and periodic fluctuations in hare abundance have not been documented in the southern range of the snowshoe hare, this pattern of habitat use and abandonment characteristic of cyclic populations has been observed during years of low hare density in Minnesota (Fuller and Heisey 1986) and Washington (Koehler 1990b). The association of hare with thickets/dense coniferous forest is well documented in other areas where hare density was similar among years (Utah, Wolfe et al. 1982; Colorado and Utah, Dolbeer and Clark 1975) or not measured (Montana, Adams 1959; Maine, Monthey 1986; Pennsylvania, Scott and Yahner 1989; New Brunswick, Parker 1984).

The mechanisms causing this shift in habitat use is a topic of current research. According to the Keith hypothesis (Keith 1974, Keith et al. 1984), the mechanism triggering cyclic hare fluctuations is starvation. As snowshoe hare densities increase, over-winter food supplies diminish in quantity and quality. A decline in hare densities begins as nutritionally stressed hares succumb to thermoregulatory stress and become vulnerable to predators. Aggression between hares (Ferron 1993) and dispersal (Boutin et al. 1985) result from food shortage. Lagging in time, the increased abundance of vulnerable prey results in an increased density of predators. Increased predation pressure then accelerates the decline and results in low hare abundance. Also, decreases in body mass during the winter affect reproduction in summer through reduced litter sizes and pregnancy rates (Keith and Windberg 1978, Cary and Keith 1979). Eventually, but lagging behind the hares, the density of predators also collapses. As the hare's food supply returns, hares again increase in density and the cycle continues. It is the time lag between vegetation, prey, and predator that keeps the populations in a cycle. If the predators could find other prey and remain at moderate densities, the hares might never experience a period of low

predation pressure where their population could reach high enough abundance to deplete their food resources and cause a cycle.

Alternatively, it appears that predation could also initiate the cyclic hare decline (e.g. Boutin 1985, Boutin et al. 1986, Krebs et al. 1986, Trostel et al. 1987, Krebs et al. 1991, 1995). Predators initially attracted by the expanding hare population would increase in density before or as the hares deplete their food resources under this scenario. An indirect effect of predation may then result in a scenario similar to the Keith Hypothesis. For example, the predators may influence the hares to sacrifice nutrition for cover (Hik 1994). Under increased predation pressure, hares are forced to spend more time in densely vegetated areas (Hik 1995). If these refugia are inadequate to support the populations until the predation pressure diminishes, starvation may ensue and lead to the Keith scenario. Boutin et al. (1985) found that most hares died on their home range rather than dispersing. Another sub-lethal effect of predation that may contribute to hare declines within the cycle is reduced reproductive output by hares, due to both maternal nutrition and maternal stress levels from foraging during periods of high predation risk (O'Donoghue and Krebs 1992, Hik 1995, Krebs et al. 1995). A lag in recovery of hares from the stress of foraging under intense predation pressure could then contribute to the cyclic decline of hares (Hik 1995 and references therein).

While the relative roles of vegetation-herbivore and predator-prey interactions within snowshoe hare cycles remains unresolved (Krebs et al. 1995), the suggestion that predation influences the use of habitat by hares remains of interest to land managers attempting to maintain configurations of habitat that support persistent hare populations. In the Yukon, starvation was evident despite experimental food supplementation (Sinclair et al. 1988, Krebs et al. 1986, Boutin et al. 1986) and Hik (1994) concluded that hares chose safer, densely vegetated habitats with less food over riskier, relatively open habitats with more food to reduce predation risk. Non-cyclic hares sacrificed food for cover by retreating into spruce bogs in central Wisconsin (Sievert and Keith 1985). Monthey (1986) and Pietz and Tester (1983) similarly suspected that hares sacrifice nutrition for cover, and Rogowitz (1988) found that cover but not browse availability correlated with hare density.

2.2.3 Influence of Predator Tactics

Insight regarding the influence of predation on hare use of refugia may be revealed by examining the hunting success and techniques of hare predators. Predators often concentrate on patches of relatively high hare density during declines (lynx, Saunders 1961, Berrie 1973, Brand et al. 1976, Ward and Krebs 1985, Brocke 1990), and migrations of other predators to areas with high prey densities are common (e.g. Craighead and Craighead 1969, Rohner 1996, Shivik et. al 1996).

On a smaller scale, the limited sight distances and difficulty of travel within brushy hare refugia may impede movements of potential predators. Although Parker (1981) cautioned that hunting success and distance to kill is related to the motivation and experience of individual predators, most information available on the predatory tactics of lynx does come from following individuals. Saunders (1961) observed tufts of lynx fur on branches and twigs within dense stands while following tracks of lynx that were pursuing hare, and noted broken canines on several skulls that he attributed to encounters with trees. Sievert and Keith (1985) observed that most predation on hares occurred in relatively open sites along forest clearings, marshes, roads, and trails. Winter kill sites had less understory cover than the mean of the study area, and kills within good (dense) habitat occurred in gaps within the dense cover. Lynx kill sites were also in openings within dense habitat in Alaska (Staples 1995) and the Yukon (Major 1989). Kills of hares by raptors doubled in open vs. brushy cover (Sievert and Keith 1985). Great horned owls were the main predators of hares in open areas in Montana (Adams 1959).

The relatively dense cover of refugia may indeed obstruct the efforts of individual predators, but these difficulties of hunting hare can be partially overcome by taking advantage of the hare's habit of traveling in the same place ("hare runs", e.g. O'Farrell 1965) or by hunting the edges of the refugia or midsuccessional patch (Todd et al. 1981, Theberge and Wedeles 1989). For snowshoe hares to persist, the inevitable losses to predators must therefore be overcome by recruitment. An average of 14.1 young per female may be produced annually (Yukon, O'Donoghue 1991), resulting in the rapid density multiplication that is characteristic of lagomorphs (up to 4,404 hares/mi² [1,700 hares/km²], Brand et al. 1976; 2,850-5,458 hares/mi² [1,100-2,300 hares/km²], Alberta, Keith and Windberg 1978; 3,194 hares/mi² [1,233 hares/km²], Kenai Peninsula, Bailey et al. 1986; 1,813-2,332 hares/mi² [700-900 hares/km²], Northwest Territories, Poole 1994). However, rapid recruitment is energetically expensive,¹⁰ and therefore necessitates a seasonal shift in habitat use.

2.2.4 Influence of Season

Aside from concealment from predators, another important benefit of cover is thermal shelter. The availability of cover likewise influences the patterns of habitat uses by hares. Cold temperatures and deep snow correlate with adult snowshoe hare mortality (Meslow and Keith 1971). Although dense deciduous vegetation can provide cover in summer, heavily stocked stands of young conifers or mature conifers with thick, low branches are optimal in winter, when hare survival strategies must balance costs of exposure to inclement weather and predators with

¹⁰The net daily energy requirements (per gram of body weight) of hares in spring exceed those of many other mammals, including mice, rabbits, humans, and cows (Kleiber 1961, in Holter et al. 1974). Even with the spring increase in available nutrition, reproduction during the summer is higher when females are in good condition at the end of winter (Meslow and Keith 1971).

forage intake requirements. Conifer thickets offer superior insulation from temperature extremes, wind, and precipitation, by providing three times the cover of deciduous thickets (Litvaitis et al. 1985b). However, hares may not require conifers for shelter from the sun (Buehler and Keith 1982), as indicated by the survival of hares in exposed pens without conifers in Alberta and Wisconsin (Keith et al. 1966), and the distribution of hares beyond treeline in Alaska and Canada. Therefore, the importance of cover for thermal shelter as an influence in patterns of habitat occupancy shelter is important, but likely intertwined with the role of cover in providing protection from predators (Buehler and Keith 1982).

As the snow melts and temperatures increase, cover for thermal protection is less important, cover in hardwood thickets increases with leaf sprouting, and predation pressure may decrease slightly (ground squirrels and marmots wake up, ungulates calves are born, migratory birds arrive, and voles are no longer protected by the snow). Snowshoe hares fuel their spring increase in metabolism (Hart et al. 1965) and reproductive activity by switching to a high energy diet of green grasses, forbs, and leaves of deciduous shrubs (e.g. Aldous 1936, Dodds 1960, Bider 1961, Wolff 1978). Because growth of high nutrient foods is often precluded by the dense coniferous refugia that provided browse (twigs, needles, stems, and bark) throughout the winter (Adams 1959, Orr and Dodds 1982), hares spend more time outside refugia during the snow-free season (Adams 1959, Wolff 1980, Litvaitis et al. 1985b). The tendency to use open areas in summer is slightly higher for females than males (Litvaitis 1990), perhaps due to the energy and nutrient demands associated with lactation. However, both resting and foraging sites may be characterized by dense canopy closure if herbaceous plants can be found underneath (Ferron and Ouellet 1992). The above strategy usually results in an increasing population during the snow-free season (Boutin et al. 1986).

2.2.5 Influence of Physiology

Throughout the year, hare protein and fat levels remain relatively constant, enough to sustain them for 4-6 days (Whittaker and Thomas 1983). Therefore, hares cannot rely on long-term alternating strategies of fattening up on nutritious items in open areas when predators are absent, and starving when predators arrive. When confronted with seasonal fluctuations in plant protein levels, hares adapt by excreting excess protein in their urine (Holter et al. 1974, Pehrson 1984b) and fecal pellets (Pehrson 1984a, Sinclair et al. 1988). The energy provided by their relatively stable protein and fat reserves fluctuates as their metabolism adjusts to the ambient temperature and costs of reproduction (Whittaker and Thomas 1983). The net effect of this process is that hares must balance their energy needs on a short-term basis (Whittaker and Thomas 1983). Because of the decreased availability of high quality food and increased thermal challenges, the process may be more critical to hares in winter. This physiological drive is reflected in the mortality of caged hares. Individuals fed inadequate diets died in 1-9 days; dying faster in colder temperatures and not surviving losses exceeding 30% of body weight (Pease et al. 1979).

Juveniles under natural conditions may not survive losses exceeding 15% of their body weight (Sinclair et al. 1982).

Given the short-term requirements of hare nutrition, it might seem surprising that hares maintain a constant intake of food despite the level of protein in their diet (Walski and Mautz 1977, Sinclair et al. 1982). However, the fluctuation of protein and secondary compounds in plants, combined with the short-term energy requirements of hares due to their limited fat reserves (Whittaker and Thomas 1983, Pease et al. 1979, Sinclair et al. 1982) may have precluded the evolution of more selective foraging strategies, especially during winter. Instead of maximizing nutrition by seeking out nutritious *species or individual* plants to browse, they appear to maximize nutrition by browsing the most nutritious *parts* of individual plants of many species (Sinclair and Smith 1984, Rogowitz 1988). Preferred diameters of less than 0.16 inches (or 4mm) have relatively high protein (Grigal and Moody 1980) and other nutrients (Wolff 1980), and have higher digestibility (Sinclair et al. 1988 and references therein). The short response time between starvation and death may explain why some studies report that hares browse plants according to availability under natural conditions (Telfer 1972, Scott and Yahner 1989, Rogowitz 1988). Thus, the hare's generalist foraging strategy complements its physiological drives/or vice versa and eventually fuels the high recruitment of hares that enable them to persist despite intense predation pressure.

2.3 Landscape Patterns and Processes and Hare Habitat Relationships

2.3.1 The Refugia Concept and Midsuccessional Forest Patches

Synthesizing concepts introduced in the preceding section, a general hypothesis of why snowshoe hares have capitalized on midsuccessional forests emerges. This structural stage may essentially be a "patch" of refugia, where the benefits of food, shelter, and concealment from predators are obtained in close proximity over a large area.¹¹ This proximity may temporarily amplify the benefits of refugia, allowing hares to increase to higher densities within dense midsuccessional patches than within patches of mature or regenerating forests containing dispersed refugia. As the density of hares increases and quality browse becomes scarce, or if the patch becomes so dense that understory branches and other vegetation is precluded, the benefits of the large contiguous patch diminish. Hares must then either starve within the patch or flee and face the predators attracted by their high densities. Also, the nutritionally stressed hares may succumb to

¹¹At a smaller scale (within-patch), interspersed openings are still desirable (winter, Morse 1939, Conroy et al. 1979; summer, Ferron and Oullet 1992).

disease or ectoparasites due to a higher probability of transmission associated with stressed, dense populations. The combined effects of predation, starvation, and disease would eventually interact to lower hare density. Over time, an area characterized by large midsuccessional patches would likely exhibit wide fluctuations in hare density under this hypothesized scenario.

The suspected relationship between midsuccessional forest patch size and hare density has been central to hypotheses concerning the cyclicity of snowshoe hare populations for nearly a century. Unlike the high amplitude fluctuations exhibited by northern hare populations, southern populations exhibit irregular, low amplitude fluctuations, or relatively stable densities (review, Wolff 1980). The contrast inspired early naturalists to speculate that dispersion of preferred habitat was responsible for stabilizing snowshoe hare populations at the southern limit of their range (e.g. Howell 1923). From Buehler and Keith (1982), Leopold (1933:64) stated: "Cycles are more severe on large continuous blocks of range than on small, dispersed, or discontinuous blocks." Dymond (1947) later commented that the cyclic nature of northern populations is the result of the "simple and uniform" northern environment, which limits the number of predators and alternative prey compared with those in the south. Grange (1949, 1965) emphasized, "only fire can create and maintain large areas of habitat for Snowshoe Hares within the Boreal Forest. It is, of course, brushy cover regeneration post-fire that comprises the most favorable hare habitat." Modern ecologists are still fascinated by the oscillations in hare abundance, but the majority of recent investigations have focused on the roles of food supply, food quality, and predation within a cycle (Krebs et al. 1995). The potential relationships between these attributes and habitat quantity and quality may nonetheless be of great importance to the land manager.

2.3.2 The Effect of Latitude on Patch Size

The implication that habitat continuity and patch size generally decrease from northern to southern latitudes intuitively follows landscape-level disturbance patterns within the range of lynx and hare. Lynx and hare ranges follow the distribution of boreal coniferous forests. As latitude decreases, these forests become restricted to increasingly higher elevations where favorable climatic conditions prevail (Brown's Law). Many differences between northern boreal forests and southern subalpine forests can be at least partially explained by the effects of increasing topography at lower latitudes. For example, boreal forests are generally more humid than subalpine forests. Although annual precipitation is lower in boreal forests, rapid evaporation at high altitudes due to lower atmospheric pressure and higher temperatures dehumidifies the subalpine forests (Knight 1994).

In both areas, the primary disturbance to initiate forest succession has historically been lightning ignited wildland fire. The importance of fire to succession in both areas is reflected in the adaptations of their vegetative communities. In the taiga, permafrost normally expands under the shade of forest canopies (Elliot-Fisk 1988 and references therein). As the active layer (distance

between permafrost and forest floor) decreases, less and less soil is available for roots. Black spruce layer branches to the ground surface for vegetative reproduction, creating a continuous fuel ladder. All that is needed is ignition. Resulting fires open the insulating forest canopy, push down the permafrost, recycle nutrients from dead material that otherwise decays at a very slow rate in the cold boreal environment, open the serotinous spruce cones, and prepare the soil conditions necessary for seed reestablishment and resprouting by vegetative species (Elliot-Fisk 1988 and references therein). In subalpine forests, the more temperate climate leads to insects, decay, and disease that interact together with fire in complex disturbance regimes.

One coniferous species adapted to the subalpine system is lodgepole pine. Due to its shade and competition intolerance, lodgepole pine is usually succeeded by other, tolerant species in absence of fire (Lotan and Perry 1983). Mortality from the mountain pine beetle results in jack-strawed logs. Under the right climatic conditions, these fuels may be ignited by lightning. Resulting fire prepares the seed bed, opens serotinous cones, removes less adapted competition, and renews succession with lodgepole pine as the dominant species (Lotan and Perry 1983).

The combination of frequent fire-igniting weather and fire-adapted vegetation translates to relatively high fire frequency under extreme fire climatic conditions. Compared to temperate forests, the average area burned is greater in boreal forests due to less abundant topographic barriers (Knight 1994). This phenomenon produces the relatively uniform structure over large areas observed in closed boreal forests (Elliot-Fisk 1988) that was recognized by the early naturalists mentioned earlier (i.e. Howell, Leopold, Dymond, and Grange). By contrast, disturbance in subalpine forests is characterized by relatively small, isolated events punctuated by larger fires when extreme fire weather ignites accumulated deadfall produced by insects and disease (see Knight 1994 for review of the dynamics of subalpine forests).

Topography has substantial influence on fire behavior (Agee 1994). On high mountain ridges and valley riparian zones, fires are less frequent due to the relatively higher capacity of these areas to retain moisture (Franklin and Dyrness 1973, Romme and Knight 1981). Therefore, fires are sometimes contained within a drainage. When fuel moisture is low, the tendency for fires to burn upslope minimizes danger to lower slopes. Under compatible combinations of fuel moisture and build-up, fires burn over ridges and spread to other drainages through spotting. The area burned in these larger fires is closer to the fires characteristic of boreal forests.

It is important to recognize that disturbance is affected by topography across the latitudes occupied by lynx. Mountainous boreal forests in western Canada may therefore exhibit patch sizes similar to southern subalpine forests. Likewise, relatively flat areas within subalpine forests may have larger patch sizes resulting from fire, such as those common in boreal forests.

The differences and similarities in median patch size between boreal and subalpine forests may be of great importance in understanding the demography of organisms whose ranges span both

zones of northern coniferous forest. As an increasing proportion of lynx and hare ranges are mapped using GIS techniques, these hypothesized habitat differences between northern and southern hare populations may be further investigated.

2.3.3 Patch Size and Cyclicity: the Case of Snowshoe Hare in Wisconsin

Given the large scales involved, it is difficult to directly test the latitude-patch theory of hare stability. However, indirect experimentation and observations may provide a useful start. In central Wisconsin, large acreages were logged and burned in the late 1800's, cleared and drained for farming and agriculture during in the early 1900's, and then abandoned during the 1930's (Catenhusen 1950 in Buehler and Keith 1982). The resulting forests have matured beyond prime hare habitat under the influence of increasing fire suppression efforts and advancing fire fighting technology. What habitat remains is reduced in quantity and isolated in area.

Interestingly, Wisconsin snowshoe hare populations that previously tracked the cyclic, high amplitude fluctuations observed in neighboring Canada no longer do so (Keith and Windberg 1978, Buehler and Keith 1982).¹² Reproduction by the non-cyclic central populations was actually higher than the northern, cyclic Wisconsin populations, primarily due to a high, sustained rate of pregnancy and a fourth litter (Kuvelsky and Keith 1983). Instead, high predation and low survival in the central Wisconsin populations was documented, and transplantation experiments demonstrated that most of the mortality occurred among "individuals moving between patches of suitable habitat" (Sievert and Keith 1985:854). The main difference in habitat between cyclic and non-cyclic populations was thought to be maturation of Wisconsin forests since the 1940's that resulted in "fragmented or island-like" habitat (Buehler and Keith 1982). Observations of hare survival in differently sized habitat patches further suggested that the probability of extinction within a patch is related to patch size and initial hare density (Keith et al. 1993).

The Wisconsin results concur with results of earlier studies in southern snowshoe hare range. In Colorado, high reproductive rates were documented, and low survival of juveniles dispersing into poor quality (open) habitats was hypothesized to prevent high amplitude density fluctuations (Dolbeer and Clark 1975). In Alberta, a much smaller decline in woodlot populations (small patch, 6:1 decline) than in neighboring forest populations (35:1 decline) was observed (Windberg and Keith 1978), and the lower peak density in woodlots was similarly attributed to high juvenile disappearance. Neither study could distinguish dispersal from predation through their techniques, but both speculated that strong predation on dispersers was the cause. New England

¹²Cycles in Wisconsin followed those in Canada from at least the early 1900's through the 1950's (Keith 1963, Buehler and Keith 1982).

cottontail survival was higher on larger than smaller patches (Barbour and Litvaitis 1993), and the perimeter-to-area ratio of habitat patches was larger for predator-killed rabbits than surviving rabbits (Brown and Litvaitis 1995).

2.3.4 Population Regulation Through Predation

Imbedded in the latitude-patch theory for explaining snowshoe hare stability is the role of predation as a density stabilizer. This subject has been reviewed by others (e.g. Wolff 1980, Sinclair 1989), so only a brief summary follows. Predators can stabilize populations if the proportion of prey that has potential to become cyclic is small (Boutin 1995). Also, if an adequate selection of alternative prey exists, generalist and mobile specialist predators may stabilize potentially cyclic prey populations by increasing their hunting activity when prey numbers are high and moving to new locations and/or switching prey when numbers are low. In contrast, specialist predators may destabilize such populations by continuing to hunt already depleted populations (Pearson 1966; Andersson and Erlinge 1977; Hansson and Henttonen 1985a, 1985b, 1989; Korpimäki 1985; Korpimäki and Nörrdahl 1989, 1991; McShea 1991). Differences in the composition and abundance of predator and prey communities may therefore be expected to influence hare density and patterns of habitat use across its range.

2.3.5 Predator Assemblages and Prey Availability According to Latitude

Along the north-south gradient in North America, there appears to be a decreased quantity of specialist predators and an increased quantity of generalist predators (Wolff 1980, Hansson and Henttonen 1985a). Also, the abundance and diversity of alternative prey increases as more niches and habitat types become available in southern latitudes. As a result, when southern predators are faced with a decline of one particular prey, they can switch to alternate species while continuing to take snowshoe hare opportunistically. The ability to switch dampens or eliminates impending consequences associated with loss of prey, unlike the boom-bust density cycles of predators in northern latitudes with limited prey choice. Because the predator populations do not show large declines, hares in southern latitudes are not often "released" from predation pressure like they are in the north. Also, many raptors migrate south in the winter (Sonerud 1986, Craighead and Craighead 1969), potentially increasing predation pressure during critical winter months. These relationships may be responsible for more stable densities in southern latitudes.

In the last 50 years, predation pressure on the snowshoe hare may have increased throughout disturbed portions of hare range, thereby further preventing or dampening potential population highs. Much of the current hare habitat in southern areas of snowshoe hare range is the result of timber harvest activities. These areas are networked by roads and trails, providing convenient

access to southern predators such as coyote and bobcats. Coyotes have increased their range and density since the turn of the century.¹³ Previously, the onset of winter may have reduced predation pressure on hares by these species somewhat, given their lack of adaptations for walking on snow [i.e. the greater surface area of a lynx paw can support twice the weight of a bobcat paw (Parker et al. 1983) and 3.4-8.1 times the foot load of a coyote paw (Murray and Boutin 1991)]. However, snow packs denser and firmer on the relatively even, hard, and exposed logging road surfaces (open areas, Murray 1991), affording less snow-equipped paws increasingly more access. Hares in winter, already stressed by decreased food availability and the trials of being a homeotherm, may thus be subjected to higher than historic predation rates under this scenario.

The effect of latitude on small mammal population dynamics has been investigated in Europe. Monitoring of small mammal abundance in Fennoscandia since the late 1940's has revealed that the tendency for arvicoline species to cycle decreases from northern to southern latitudes (Laine and Henttonen 1983; Hansson and Henttonen 1985a, 1985b). In the south, these populations showed annual fluctuations (Hansson 1979) whereas in north they showed classic 3-5 year cycles (Henttonen et al. 1977; Hörnfeldt 1978; Hansson and Henttonen 1985a, 1985b, 1989). In southern Fennoscandia, there is a larger selection of alternative prey with practically year-round availability, a higher density of generalist predators, and a more heterogeneous environment than in northern Fennoscandia (Erlinge et al. 1983, 1984). Generalist southern predators switched prey when prey densities fluctuated, thereby maintaining constant population size (Erlinge et al. 1983, 1984; Korpimäki 1989; Korpimäki and Nörrdahl 1989, 1991). As previously discussed, time delays in predator response are often characteristic of unstable predator/prey relations (e.g. Keith et al. 1977). Northern generalist predators showed such time delays, perhaps due to a lack of alternative prey. In both latitudes, specialist predators responded numerically to the abundance of prey.

Akçakaya (1992) developed a model based on the ratio of predators to prey to explain the 10-year period of hare cycles and latitudinal gradient in cyclicity. The effects of predator and prey community composition are balanced by using the ratio. Although hares produce larger litters in northern latitudes, total production by hares in both areas remains similar. Therefore, mortality is higher in the south (Keith 1966b). Habitat managers should be aware of the potential influence of predators on hare habitat use and experiment with landscape design to facilitate snowshoe hare survival in southern latitudes.

¹³ The extirpation of wolves in southern latitudes may have also contributed the expansion of coyotes and bobcats (Litvaitis and Harrison 1989 and references therein).

2.3.6 The Search for the Definition of Optimal Hare Habitat, Incorporating Time

Most studies of snowshoe hare habitat preferences do not allow determination of optimal hare habitat because they report habitat quality as a function of the density of hare recaptures, pellets, or tracks. For example, the hare's close association with midsuccessional forests reflects the influence of cover on habitat selection. However, this selection may involve sacrifices of forage, especially in winter and/or under intense predation risk. As argued by Van Horne (1983), density is not always a reflection of habitat quality. To assess habitat quality, survival, reproduction, and movements among habitats must also be investigated.

2.3.6.1 Homogenous vs. Heterogenous Habitats

Previous paragraphs have presented arguments suggesting that large patches of midsuccessional forests support high hare densities, and perhaps lynx. In northern latitudes, this situation seems to favor cyclic over stable hare populations. General ecology suggests that homogeneous habitats provide fewer niches and support fewer species than heterogeneous habitats with greater niche availability. In the former environment, one species may dominate, creating a potentially unstable situation if the population periodically devours its limited resources, as observed in northern snowshoe hare populations (e.g. Keith Hypothesis). Dense populations may also rapidly succumb to diseases due to the potential ease of transmission. Evidence for the relation of cyclic behavior to restricted niches is demonstrated by members of the arvicoline family. In species with narrow niches, like the tundra vole, cycling has been observed (Whitney 1976, Krebs and Wingate 1985), whereas species with variable and/or wide niches, such as the northern red-backed vole, have shown less evidence of cycling (Whitney 1976, West 1982, Fuller 1985, Krebs and Wingate 1985).

The diversity of a heterogeneous environment may facilitate stability by providing an array of alternatives should any particular species crash or resource be depleted, as hypothesized for some small mammal communities (Pruitt 1968, Bondrup-Nielsen 1987). Alternatively, habitat heterogeneity may promote stability because populations are unable to reach high enough densities to cycle in such environments (Bondrup-Nielsen and Ims 1988). In either case, the vulnerability of prey to predators in homogenous vs. heterogeneous habitats may also influence prey stability (2.3.6.1). The definition of "optimal" habitat becomes gray: is it better to reach higher but fluctuating densities in large patches of midsuccessional forest or lower but stable densities in heterogenous older forests?

2.3.6.2 Snowshoe Hare and Mature Forests

In mature forest snowshoe hare habitat, heterogeneity that provides cover and browse may arise from a number of situations: 1) small conifer thickets may remain from the previous successional stage, 2) individual trees with branches that extend down the bole to the forest floor may exist in fairly open stands, and 3) vegetative thickets may grow within gaps between the forest canopy, or 4) clumps of vegetation may collect as understory (shade tolerant climax species). Thus, hare use of a relatively open forest characterized by an understory of preferred refugia may be statistically equivalent to a more uniform and dense forest. For example, Engelmann spruce forests that contained islands of regenerating subalpine fir were statistically indistinguishable (highly variable pellet counts per transect) from relatively more open spruce sites, despite the average number of pellets within the pure subalpine fir sites being six times higher than the mixed fir-spruce sites (Utah, Wolfe et al. 1982). Within Alaskan white spruce forests, hare activity was noted where white spruce trees had branches within 6.4 feet (2 m) of the ground near alder thickets and also where squirrels had clipped numerous spruce tips onto the snow, but overall hare density was twice as high in the nearby fire-regenerated midsuccessional forest (Staples 1995). Other studies suggest that mature forests possessing understories with structure conducive to sustaining hare densities often support densities of hare similar to but slightly lower than a relatively uniform midsuccessional stand (Dolbeer and Clark 1975, Thompson and Colgan 1987, Thompson et al. 1989, Mowat and Staniforth 1995 *in press*).

The association of hare within refugia in mature forests may prove to be critical over time. Dispersed refugia provide an effective solution to the fundamental habitat problem of snowshoe hare, i.e. that forests grow. The combination of short stature and high nutrition requirements subjects snowshoe hares to another constant pressure, that of forest maturation. As nutritious small stems and needles grow into higher and less accessible canopies, hares must seek forage elsewhere. Likewise, shelter and predator concealment also rise with the forest canopy. These factors become increasingly important in the winter, if understories are buried beneath the snow and temperatures drop. Unless succession is reinitiated in such areas, refugia within the forest become the only areas left for hares to occupy.

Mature forest refugia may effectively distribute hares across a landscape, thereby providing colonizers to exploit new patches of midsuccessional habitat created by wildland fire as they arise. Nonetheless, hares reach consistently higher densities in midsuccessional patches than mature forests, as demonstrated by the high density of hares within lodgepole pine communities (Koehler et al. 1979; Sullivan and Sullivan 1982, 1983; Koehler 1990b; Slough and Ward 1990; Swayze 1995).

2.3.6.3 Snowshoe Hare Vulnerability and Lynx

For lynx, high quality habitat translates to habitat that supports a high density of *available* prey. Current evidence relating lynx hunting success to available habitat types appears to provide conflicting inferences concerning the lynx's perspective of hare habitat quality. Two studies in southern Yukon concurred that lynx prey chases occurred in habitats according to habitat availability.¹⁴ However, Major (1989) found lynx to have highest hunting success in mature pine habitats and Murray et al. (1994) found no difference in success among habitat types.¹⁵ The overall success rate of 30% observed by Murray et al. (1994) was approximately equivalent to the lowest success rate (33%) recorded by Major (1989; regenerating lodgepole pine).

The high overall success rate (57.1%) in at least part of Major's (1989) study area was accompanied by extremely high lynx densities (57.6/100km², Teslin Burn, Slough 1995), compared to a high density of 17.1 lynx/100km² in Murray et al.'s (1994) study area (Kluane, O'Donoghue and Hofer 1995). Hare density fluctuations also reached higher densities in the Teslin Burn (12-13 hares/ha, Slough 1995) than Kluane (2.34 hares/ha, O'Donoghue and Hofer 1995) and maintained higher densities during hare lows (~1 hare/ha vs. 0.08 hares/ha).

The study areas apparently differ considerably in vegetation. Major's (1989) habitat data came from Slough and Ward's (1990) telemetry data, where the study area was mainly a midsuccessional forest of regenerating lodgepole pine (Teslin Burn). Murray et al. (1994) characterized their study area as mostly mature spruce forest (>61% open to very open), with only 2% very closed spruce.

As investigators of the Teslin Burn research project complete their final analyses and investigators of the Kluane research project and continue their work, potentially enlightening lynx habitat relationship inferences may arise. In addition to vegetation differences between study areas, the influence of snow characteristics between study areas, season of study, and the age structure of the hunting population (i.e. adults vs. yearlings, Parker 1981) are enough variables to produce conflicting results. Meanwhile, it appears that lynx may show different responses to various habitat configurations, and that a variety of habitat types may be necessary to sustain lynx populations. Until the interactions of prey-predator-habitat are further clarified,

¹⁴The studies were conducted at similar times (1987-89, Major 1989; 1988-1990, Murray et al. 1994), but they employed different methods. Murray et al. (1994) used snow tracking only (348 miles, 560 km) whereas Major (1989) used a combination of snow tracking (37 miles, 60 km) and telemetry locations.

¹⁵Similar to Major's (1989) results, lynx in regenerating spruce habitats on the Kenai Peninsula had higher hunting success in mature forests adjacent to regenerating habitat where the density of hares was 50% lower (0.38 kills/pursuit vs. 0.17 kills/pursuit, Staples 1995). Parker (1981, Cape Breton Island, Nova Scotia) noted higher success in more open forests in a landscape dominated by older seral stages, but more chases and kills in the advanced successional habitats that were present.

land managers should work towards creating a diversity of habitat types and configurations, so that hares are not only available in high numbers (larger patch) but also available over broad areas (small patches within and between mature forests) with differences in accessibility by lynx (for hunting success).

2.3.7 Synopsis

In boreal forests, a decline in hare density eventually leads to reduced predator density because no or few other prey species are available during winter for the predators to switch to (van Zyll de Zong 1966, Keith et al. 1977). Hare populations that survive in refugia or midsuccessional patches will keep reproducing and attempting to disperse. Eventually, some hares may survive when leaving their refugia under the decreased predation pressure, and expand the number of occupied habitats. Successful dispersal would distribute hares across the landscape so that individuals would be available to recolonize newly emerging midsuccessional habitat. Subsequently, higher hare numbers might influence the recruitment and immigration of predators, enabling the predator density to increase.

With an increase in predators, hares might retreat to their refugia (Windberg and Keith 1978, Wolff 1980, Hik 1994). If the occupied habitat patch is large enough, predators might reduce the total number of hares within the patch without exterminating the patch itself. Because it is difficult for winged or larger, wide-bodied predators to maneuver through vegetative thickets, predators would concentrate on edges and open gaps within the patch. Compared to larger patches, small patches of occupied habitat may support smaller numbers of animals and have increased risks of loss due to predation: increased perimeter-to-area ratios may render relatively more hares vulnerable to edge-hunting predators. Therefore, predation may be a more effective density stabilizer in a landscape characterized by small patches than large patches.

At lower latitudes, it may take a relatively large patch of hare habitat to enable the hares to overcome the intense predation pressure and effectively increase their density, because predators on the southern margin are mostly generalists and therefore able to maintain populations by switching to other prey when hare densities are low. Within large patches, however, high density hare populations may consume available food supplies, affecting plant responses and causing cyclic declines. Also, denser populations may face increased risks of disease due to a combination of ease of transmission and nutritional state of individuals.

2.4 The Effect of Landscape Level Hare Dynamics on Lynx

Three hypotheses concerning the effect of landscape level hare dynamics on lynx have subtle management implications related to how lynx use space. These are important to consider when

trying to increase or maintain lynx within a defined area, such as DNR's jurisdiction within lynx range in Washington.

2.4.1 The Prey Density Hypothesis

Traditional carnivore ecology predicts that lynx adjust the size of their home ranges according to prey *density*, with the boundary of home ranges defined by the area required to support enough hares to supply their metabolic needs. The size of this area would change through time as prey density fluctuates and alters the amount of habitat required to sustain an individual.

As an analogy, lynx home ranges can be compared to a rubber band. With plenty of food, the rubber band remains small. As food supplies decrease and disperse, the rubber band stretches. The lynx home range rubber band is currently thought to be quite stretched in Washington, despite uncertainty in whether home ranges here are statistically larger than elsewhere (WDW 1993).¹⁶ Therefore, land managers are guided to increase forest conditions that support lynx food supplies over time to increase the probability that lynx will persist (Washington, WDFW 1996).

However, to obtain forage habitat, the "missing element" in current lynx range (WDW 1993, WDFW 1996), a stand must proceed through a "non-habitat" phase, because lynx and hare generally avoid open areas. The introduced non-habitat could then stretch the lynx's home range even further. If too much non-habitat were created too quickly, currently resident lynx might emigrate or starve, creating localized extinction. This would be somewhat equivalent to stretching the rubber band until it breaks. Also, transforming a large portion of a landscape into one common age class would result in large areas maturing beyond the useful stage simultaneously. The object of lynx-sensitive forest management would then be to increase forage habitat *slowly*, allowing slight stretching of the home range rubber band but not breaking it. The density of lynx would increase with creation of forage habitat, through shrinking the average space required per lynx.

¹⁶Interestingly, 10/22 animals in Brittell et al. (1989) and Koehler (1990a) had mean home ranges less than 15 mi². The exclusion of the substantial portion of smaller home ranges may have been the result of averaging data. In such small sample sizes, the median will give a superior indication of central tendency than the mean, as the mean will be influenced by the outlying data. However, even if we assume that home ranges in Washington are most often 15-40 mi² (or 39-103 km²), this range is similar to home ranges reported elsewhere. WDW (1993) confirmed this conclusion by summarizing that approximately the same number of home ranges reported in the literature were larger (4/11) as smaller (5/11) than Washington's. The number of studies reporting lynx home ranges smaller than Washington's in WDW (1993) is further reduced when the average home range of lynx in the Soviet Union (where the resource base is different) and the snow tracking studies (result in smaller home ranges than telemetry methods) are excluded from the summary.

2.4.2 The Resource Dispersion Hypothesis

Another hypothesis, first developed in the field of ornithology and later applied to carnivore sociology (MacDonald 1983), predicts that although the density of prey may be the primary influence on lynx density, the *dispersion* of prey is the primary influence on home range size. According to this hypothesis, individuals concentrate their activities in an area that represents a compromise between having enough *patches* of prey for survival, but not so many that they cannot be defended. The minimum territory size and configuration is determined by the spatial arrangement of available prey patches rather than prey abundance. Lynx home ranges would thus be relatively stable through time, with their size correlated to the dispersion of patches.

As prey density increased within the patches of an individual home range, the density of predators that could be supported would increase. Abundant prey would facilitate recruitment. Offspring might then be allowed to occupy part of the area originally dominated by the parent. The advantage to the parent would be that the prey resource is shared with relatives rather than unrelated immigrants, thereby increasing the parent's fitness. As prey availability within the patches declines, dispersal would ensue, leaving the founding individual, or perhaps its social superior, to maintain the original range.

The object of lynx-sensitive forest management under the Resource Dispersion hypothesis would be similar to the prey density hypothesis, i.e. slowly increase the number and quality of prey patches. However, the density of lynx would increase through the number of lynx per area, rather than shrinking of home range. Small home ranges would be the function of the dispersion of prey patches, with smaller home ranges occurring where the distance between patches is relatively short. Land managers would plan management activities with the understanding that the whole area was potentially occupied and stable, rather than constantly identifying home range areas around the landscape. This would require planning for some "permanent" landscape features, such as travel corridors, to provide lynx with routes to reach current prey habitat within a management area.

2.4.3 Core Density Hypothesis

The Resource Dispersion Hypothesis corresponds with a recent hypothesis concerning lynx population dynamics by Breitenmoser et al. (1993). In the context of a fluctuating prey resource, the motivation for reducing home range size with prey density diminishes. Hares don't remain at peak or high densities for very long. Perhaps fewer than 4-5 years of a 8-11 year hare cycle (Brand et al. 1976) will supply enough hares to fuel successful lynx reproduction. Therefore, just after an individual lynx adjusted its territory size to accommodate the higher hare densities, hare density would decrease and force the lynx to expand its territory again. However, other lynx in

the area might also be expanding their movements due to the hare decline (Ward and Krebs 1985, Bailey et al. 1986, Poole 1994), increasing the potential for intraspecific interaction.

Heightened aggression during periods of low prey density has been documented in wolves and foxes (see MacDonald 1983 and references therein). Such interaction has not yet been documented for lynx in North America, but accounts of lynx preying on other lynx in North America (Elsey 1954, O'Donoghue et al. 1995, Slough 1995, Poole 1995) and aggression associated with breeding in European lynx (Guggisberg 1975) suggest that it is possible. Territoriality was suspected to influence lynx use of habitats relative to availability on Cape Breton Island (Parker 1981). Thus, it might be advantageous for resident lynx to maintain one territory at all times, defined by the availability of prey at lows in the hare cycle (i.e. defense less costly than offense).

In the Yukon (Breitenmoser et al. 1993), observations that resident lynx home range size or overlap didn't change when lynx densities expanded 10-15x following an increase in hare density¹⁷ (one lynx male occupied the same home range for at least ten years) led to the idea of a "core population." This low density resident population is thought to persist through lows in hare cycles and display low reproduction in times of low prey availability, much like lynx at the southern edge of their distribution (Washington, Brittell et al. 1989 and Koehler 1990a). However, when hare density increases, individuals within the core population profit by increased reproductive success. Up to eight kittens can be produced by one female lynx during peak hare years (M. Fuller, pers. commun. in Breitenmoser et al. 1993), with a mean litter size of 5.3 kittens for adults and 4.2 for yearlings at peak hare densities (Mowat et al. 1996b).

The fundamental distinction of this hypothesis is that lynx exploit hare cycles and not vice versa. Adult lynx attempt to reproduce every year (Mowat et al. 1996a), so that kitten survival is the important recruitment variable. Before changes in adult litter size are seen in response to hare densities, kitten survival is near zero (Mowat et al. 1996b). The ability of lynx to rapidly recruit young in good years is unique in the cat family, along with the domestic cat. Mowat et al. (1996b) interpret this as an adaptation to fluctuating prey, similar to Arctic fox.

As predicted by the Resource Dispersion hypothesis, there are some indications that related lynx settle close to one another. Breitenmoser et al. (1993) observed philopatry in female kittens (but dispersal in males). G. Mowat (Lethbridge Community Coll., pers. commun.) observed three generations of female lynx in one natal area (Yukon). On the Kenai Peninsula, adult lynx were found together outside of the breeding season on at least four occasions (Staples 1995). This

¹⁷Brand et al. (1976) also noted that although lynx appear to separate in space and time, this doesn't limit lynx density.

sharing of home ranges among core-population lynx may be difficult to detect because the outer-most 5%-10% relocations are usually excluded from home range overlap and size assessments. Superficially, home ranges might then appear like they decrease with lynx density (kitten addition) in the short-term. Lynx are known to separate in space and time (Brand et al. 1976), so perhaps the core population residents visit the outskirts of their territories infrequently.

When hares again decline, both the Prey Density and Resource Dispersion/Core Density hypotheses predict that the number of animals occupying an area must decrease. Perhaps inferior animals leave first, leaving the original territory to the resident adult. Alternatively, the family group could stay intact and hunt together (Barash 1971, Carbyn and Patriquin 1983, Breitenmoser et al. 1993, Staples 1995). In the latter case, young males might stay within the family group, as there would no longer be motivation to leave and seek reproductive opportunities (males increase their home ranges with hare density in Yukon, Slough and Mowat 1993). However, hares may decline past a threshold where even core population lynx cannot maintain their territories, as evidenced by nomadism and starvation at extremely low prey densities (Poole 1994). Breitenmoser et al. (1993) observed some yearlings staying in the parental home range after a hare crash, whereas the adults emigrated.

Overall, it is difficult to analyze published lynx studies to assess this hypothesis because most studies are not long enough in duration to address long term spatial behavior of lynx and few studies are able to assess relatedness of neighboring lynx. Nonetheless, Brand et al. (1976) noticed that lynx home range sizes were stable through fluctuating prey densities in Alberta, but Ward and Krebs (1985) and Poole (1994) reported an inverse relationship between hare density and lynx home range size. Perhaps a combination of the two hypotheses occurs in time (i.e. with the hare cycle) and space. Perham (1995) reported that lynx with quality patches of prey maintained their home ranges while others lacking such patches became nomadic. As standardized methods are employed to monitor hare populations (e.g. Krebs et al. 1987), a threshold hare density might be found where lynx emigrate rather than maintain home ranges.

2.4.4 Do lynx in Washington Follow the Resource Dispersion and Core Density Hypothesis?

One implication of these hypotheses is that lynx in southern areas may be stable, "core" populations existing at low densities, displaying low reproduction, and occupying stable territories, with sizes reflecting the dispersion of prey within the area (Breitenmoser et al. 1993). Should hare density increase and or new territory become available (e.g. post-fire), these lynx could successfully exploit resulting hare populations and display temporary high recruitment.

No studies have occurred in Washington to sufficiently address the long-term population dynamics or spatial distribution of lynx within the state. Nonetheless, the initial information provided by previous studies is provocative. As for the stability of territories in Washington, Koehler (1990a) observed lynx using the same home ranges for >2 yrs. Lynx in Washington are certainly at low densities; however, these low densities are not the lowest recorded in North America (Fig. 5). Instead, they fall within the range of reported lynx densities during population lows across lynx range. Lynx densities are much more variable at peak lynx densities, with peaks reported from 10-57 lynx/100km² (Brand and Keith 1979; Parker et al. 1983; Bailey et al. 1986; Poole 1994; O'Donoghue and Hofer 1995; Slough 1995). This variation might be expected because the highs of hare abundance do not always reach the same peaks at different locations (Smith 1983), and hare density is somewhat local phenomenon depending on climate, habitat quality and quantity, and quantity and quality of predators. Perhaps the consistent low densities of lynx reflect the maximum density of lynx that can survive on a combination of scarce hares and alternative prey, i.e. a "core-population".

Does the dispersion of prey patches influence the density of lynx in Washington? Brittell et al. (1989) reported that lynx incorporated habitats into their home ranges according to availability. However, larger home ranges were correlated with habitat variables that indicate dispersion of prey habitat (e.g. rock or talus slopes, WNW and NNW aspects, and larger proportions of mature forest. This observation suggests that prey habitat configuration may indeed be a vital component of habitat quality. The relationships surrounding optimal habitat configurations given vegetative composition remains for future researchers to decipher.

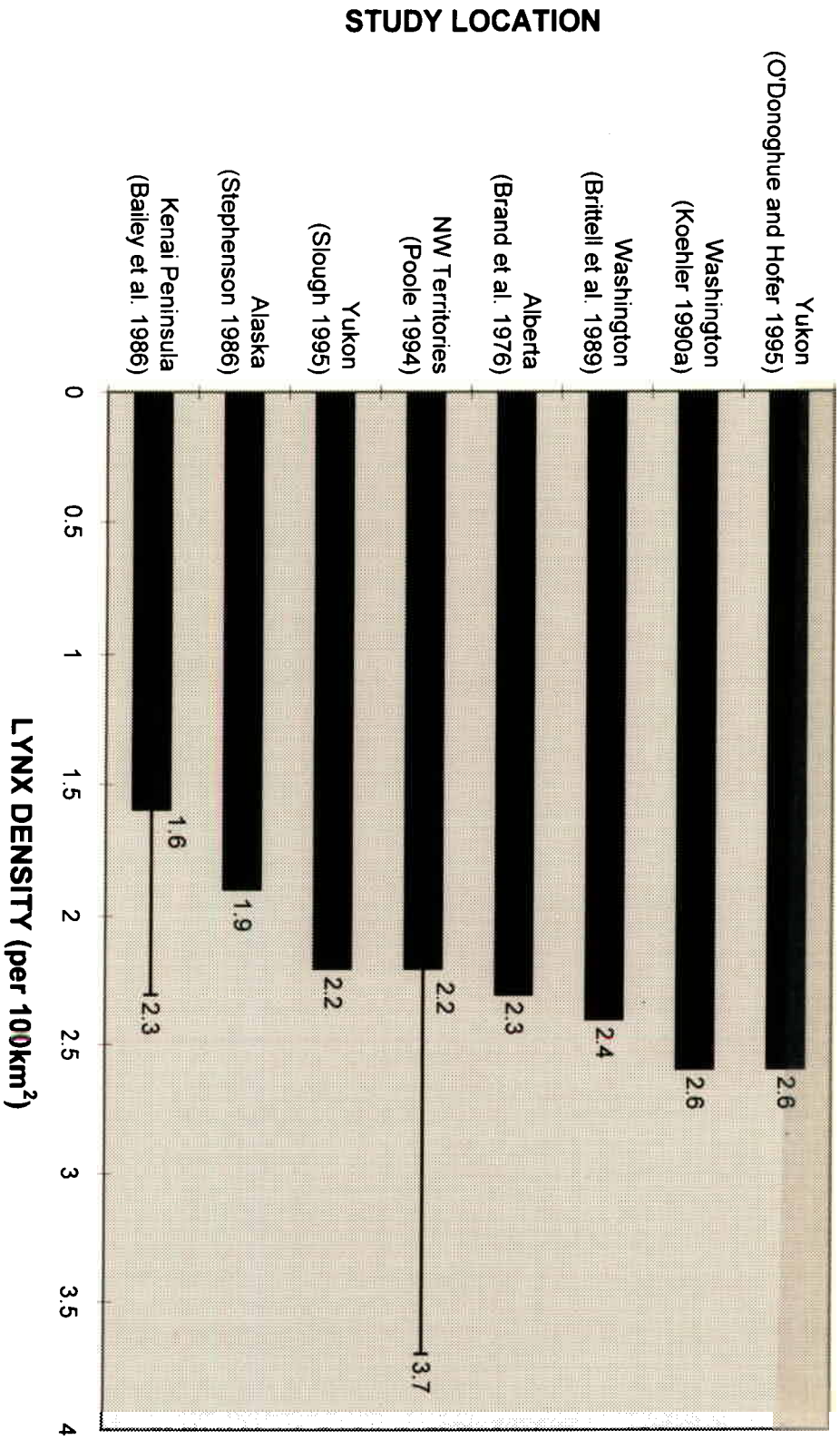


Figure 5: Lynx densities reported in the literature. Densities from outside of Washington represent densities at cyclic population lows. Error bars represent ranges.